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BIOTA OF FRESHWATER ECOSYSTEMS. IDENTIFICATION MANUAL NO. 1. FRESHWATER PLANARIANS (TURBELLARIA) OF NORTH AMERICA

Roman Kenk

Smithsonian Institution
Washington, D. C.

February 1972

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A key is presented for the identification of the species of North American freshwater triclads or planarians known at present. Introductory chapters deal with the collecting, culturing, preservation, study, and general organisation and life cycle of planarians. The key is followed by a listing of the species and subspecies, giving their distinguishing characteristics, ecological requirements, and geographical ranges. Illustrations depict the external appearance and diagrams of the reproductive organs of the individual taxa. The principal literature for each species is indicated and listed in the appended bibliography of 65 items. An index of the generic and specific names and synonyms concludes the report. One new subspecies, *Polycelis coronata brevipenis* is established for L. H. Hyman's *Polycelis coronata*. (EPA)

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Identification Manual No. 1

FRESHWATER PLANARIANS (TURBELLARIA) OF NORTH AMERICA

by

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for the

ENVIRONMENTAL PROTECTION AGENCY

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FOREWORD

"Freshwater Planarians (Turbellaria) of North America" is the first of a series of identification manuals for selected taxa of invertebrates occurring in freswater systems. These documents prepared by the Oceanography and Limnology Program, Smithsonian Institution, for the Environmental Protection Agency will contribute toward improving the quality of the data upon which environmental decisions are based.

Additional manuals will include, but not necessarily be limited to, freshwater representatives of the following groups: amphipod crustaceans (Gammaridae), branchiuran crustaceans (*Argulus*), isopod crustaceans (Asellidae), decapod crayfish crustaceans (Astacidae), leeches (Hirudinea), polychaete worms (Polychaeta), aquatic dryopoid beetles (Dryopoidea), and freshwater clams (Sphaeriacea).

ABSTRACT

A key is presented for the identification of the species of North American freshwater triclads or planarians known at present. Introductory chapters deal with the collecting, culturing, preservation, study, and general organization and life cycle of planarians. The key is followed by a listing of the species and subspecies, giving their distinguishing characteristics, ecological requirements, and geographic ranges. Illustrations depict the external appearance and diagrams of the reproductive organs of the individual taxa. The principal literature for each species is indicated and listed in the appended bibliography of 65 items. An index of the generic and specific names and synonyms concludes the report. One new subspecies, *Polycelis coronata brevipenis*, is established for L. H. Hyman's *Polycelis coronata*.

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SECTION I

INTRODUCTION

The present report is a review of the species and subspecies of the North American freshwater triclads or planarians known at the present time. It should not be considered to give a definitive picture of the planarian fauna of the geographic area covered, north of Mexico, as many parts of the continent are still little explored with regard to lower aquatic invertebrates. This is particularly true for large sections of the West and South of the United States and the greater part of Canada.

It was considered appropriate not to limit the review to a simple key. When attempting to identify a given species through a key, one ends up with a specific name which one must accept on good faith. Should one happen to have an undescribed species at hand, it would, in most cases, key out to a known species. In order to avoid this pitfall, every species is treated separately, its distinguishing external appearance and anatomical features are described, and the principal literature sources which may lead to a more detailed description of its morphology and ecology are listed. In this way it should be possible to avoid the uncertainties inherent in the use of simple dichotomic keys and to have a means of either confirming or questioning the correctness of the identification.

In addition to the valid names of the individual species, all synonyms which have been used for the American planarians are listed in the species descriptions, giving the name of the author and the date of the first publication of each synonym.

Planarians have played a certain role in the biological assessment of water quality in Europe. Some species have been found to be very sensitive to organic and inorganic pollution of their habitats while others tolerate mild degrees of pollution. In general it may be said that planarians are intolerant to the presence of heavy metal salts in the water. Little has been done in the study of American turbellarians with regard to their behavior toward pollutants. The American fauna of planarians differs from that of Europe, and no native species is common to both continents. One American species was introduced in Europe at the beginning of this century, and one imported European species was discovered recently in North America. It is, therefore, not possible to apply the results obtained by European workers to the American planarian fauna without detailed field observations.

It is hoped that the present report will be useful in any future systematic investigation using the presence or absence of planarians in the evaluation of water quality in North America.

COLLECTING

Planarians are, in general, negatively phototactic animals, hiding in daytime in dark places. They may be collected by examining the undersides of flat stones and other objects (fallen leaves, pieces of wood etc.) or the stems of submerged or partially submerged water plants. The planarians are then removed from the substrate with a soft paintbrush or the moistened ball of a finger (carefully, without exerting any pressure), placing them immediately in a jar containing water taken from the same habitat. Where there is dense vegetation or an accumulation of leaf litter or other debris, samples of these may be taken in a glass jar filled with water; after keeping the jar in a cool place, usually overnight, planarians, if present, will tend to accumulate in the upper layer of the water and may be collected with a wide-mouthed syringe fitted with a rubber bulb. Many planarian species can be attracted by bait (a piece of liver, meat, a dead frog, fish, crushed snails or earthworms) placed under a flat stone and examined after several hours. A very effective method is that of placing the bait in a glass or plastic jar with a lid bearing many small round perforations (of 3-5 mm diameter). The jar is then submerged in a shaded location in a stream, pond, or lake and left for some time. Upon retrieval, usually after 24 hours, planarians will be found inside the jar while larger scavengers, such as crayfish, have been kept out. This method is applicable also in lakes at greater depths if the bait jar is submerged, together

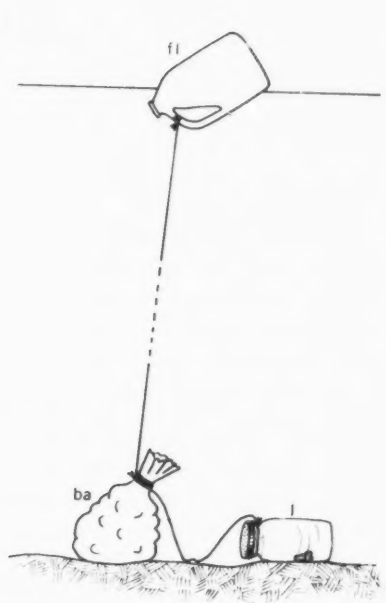

Fig. 1. Baiting of planarians in lakes. ba, canvas bag with stones; fl, float; j, jar with perforated lid containing bait.

with some anchoring ballast, and attached by a line to a float (Fig. 1). Not all planarian species will be attracted to dead bait. Some species,

e.g. *Procotyla fluviatilis* and some subterranean planarians, apparently do not react to chemical food stimuli but rather to vibrations produced by their living prey, such as small crustaceans and insect larvae. Other methods of securing deep-water planarians are by means of a bottom grab sampler or by a trawling dredge equipped with a canvas bag which skims the upper layer of mud or silt; the planarians may be separated by using sieves of proper mesh size.

TRANSPORTING AND CULTURING

Some species of planarians can be identified by an experienced collector with reasonable certainty in the field. In many cases, however, it is necessary to transport them to a laboratory or even to send them, preferably alive, to a specialist. As many planarians, particularly those living in cold springs, deep lakes, or in subterranean habitats (caves, groundwater), are very sensitive to temperature fluctuations (stenothermic), they should be transported in well-insulated containers. Vacuum-insulated (thermos) bottles are quite appropriate and may be used also for the shipping by air mail (special delivery) across the continent, provided they are taken care of immediately at the point of destination (they should not arrive at a laboratory on a weekend).

Some planarians cannot be identified by their external features alone but require the study of anatomical characters, specifically an analysis of their reproductive organs. Unfortunately, many of the specimens collected in the field are sexually immature. It is important, therefore, to select the largest individuals from a given population for further study and identification. Should there be no mature animals available, it is often possible to raise young animals to maturity in laboratory cultures.

Culturing is carried out in shallow glass aquaria (finger bowls) or in enameled pans kept in the dark or in dim light at proper temperatures, according to the tolerance limits of the species. The water should be changed every two or three days when kept at room temperature and about once a week in refrigerated cultures. Spring water or filtered pond water may be used, but chlorinated tap water should be avoided unless the chlorine has been removed by appropriate chemicals (e.g., sodium thiosulfate, the photographic "hypo"), by letting it stand for 24 hours in an open container, or by bubbling air through it. The planarians may be fed once or twice a week. Most species will accept small pieces of liver, meat, clotted blood, cut-up earthworms, or living food such as the oligochaete *Tubifex* (obtainable in pet stores as fish food). A few species refuse dead food but attack living small crustaceans (*Gammarus*, *Asellus*, *Daphnia*, etc.). The food is left in the aquarium for several hours, then removed, the water changed, and, if necessary, the aquarium cleaned. Planarians are capable of surviving extended periods of starvation, several months, particularly when kept at low temperature. When starving, they gradually grow smaller, their anatomical makeup is simplified, their entire reproductive system is reduced, and they become indistinguishable from young animals.

PRESERVATION

The soft, very delicate and flexible body of planarians can easily be injured and distorted. It is very difficult to preserve its natural shape, particularly the shape of the anterior end or head, which is of some taxonomic importance. Animals killed with alcohol or formalin are often badly contracted and twisted and are difficult to study. The fixing method should preserve the animal well extended. The method recommended by Hyman (1953a:128) is to place the planarians in a very small amount of water, kill them stretched out with 2% nitric acid followed by 70% alcohol (or any other fixative). De Beauchamp (1932:126) uses a mixture of ethyl alcohol (70%, 7 parts), formalin (2 parts) and glacial acetic acid (1 part) into which the animals are dropped individually; after several hours the fixative is replaced with 70% alcohol. Recently Carpenter (1969b) has developed a method of rapid freezing of the extended animals. My favored method is to kill the extended planarians, while they are in gliding motion in very little water, by pouring over them a hot, almost boiling, fixative, preferably a saturated solution of corrosive sublimate (mercuric oxide, $HgCl_2$) in water or saline, with a subsequent addition of a few drops of diluted acetic acid; after fixing for 4-24 hours the animals are first washed in water, then transferred to increasing strengths of alcohol until a concentration of 70% to 80% is reached in which they may remain until further treatment; the last traces of sublimate are removed by adding small amounts of tincture of iodine to the alcohol until the color remains stable.

None of these methods gives ideal results since there will always be some contraction or distortion of the body or of internal organs. For anatomical study, simple shrinkage is better than twisting.

PREPARATION FOR ANATOMICAL STUDY

Whole mounts of planarians, stained or unstained, may be prepared by the usual techniques but are of limited value in the analysis of anatomical structures. They will show the number and arrangement of the eyes, the configuration of the digestive system, and possibly some parts of the reproductive system (testes, ovaries, copulatory organs). Details of the anatomy must be studied in microtome sections.

The specimens are embedded in paraffin or a combination of celloidin and paraffin and serial sections of 5-10 microns thickness are prepared. For the purpose of species identification, sagittal sections are most suitable, transversal and horizontal sections may be useful if sufficient material is available. The choice of histological stains is optional according to the preference of the investigator. A good staining method for the general study and the analysis of muscles and glands is a combination of hematoxylin and eosin.

GENERAL FEATURES

Planarians or freshwater triclads are elongated, flattened Turbellaria, the native American species measuring in length from about 2 mm (freshly hatched) to perhaps 40 mm. In the extended, quietly gliding animal one distinguishes an anterior portion or head, often characteristically shaped, bearing important sense organs. The lateral margins of the head may protrude as auricles (which have chemical and mechanical sensory receptors). There are usually two dark eye spots on the head, each located near the medial margin of a white area, often accompanied by smaller accessory or supernumerary eyes. Some species have numerous eyes and subterranean planarians are often eyeless or blind. A median adhesive organ may be differentiated on the frontal margin of the head. The body may or may not be pigmented, often exhibiting various patterns of pigment arrangement. The mouth (m), which serves also as anus, is situated in the midline on the ventral surface, far removed from the head; the gonopore or genital aperture is found in the space between the mouth and the posterior end.

The body is covered with a ciliated epidermis containing rhabdites, small rod-like structures which, when discharged, produce abundant mucus. The

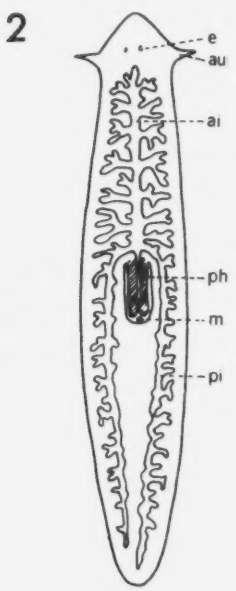

Fig. 2. Digestive system of a planarian. ai, anterior intestinal ramus; au, auricle; e, eye; m, mouth; ph, pharynx; pi, posterior intestinal ramus.

digestive system (Fig. 2) is a gastrovascular cavity with three main divisions (one anterior and two posterior intestinal rami, ai and pi) from which many lateral branches originate. In the prolongation of the anterior ramus is a muscular cylindrical pharynx (ph) lying in a separate chamber, the pharyngeal pouch. When feeding, the pharynx is pro-

truded through the mouth opening. A few American species have, besides the principal pharynx, multiple pharynges attached to the anterior portions of the posterior intestinal rami, which project into the common pharyngeal chamber (polypharyngeal species).

The space between the epidermis with its underlying basement membrane and the gastrodermis or intestinal epithelium is filled with a loose parenchymatous tissue or mesenchyme in which the remaining organs are embedded. The central nervous system if formed by a pair of cerebral ganglia or brain in the head, from which a pair of ventral nerve cords extend to almost the posterior end, connected by numerous transverse commissures. From these parts originate many nerves running to various organs and to a nerve plexus located below the epidermis.

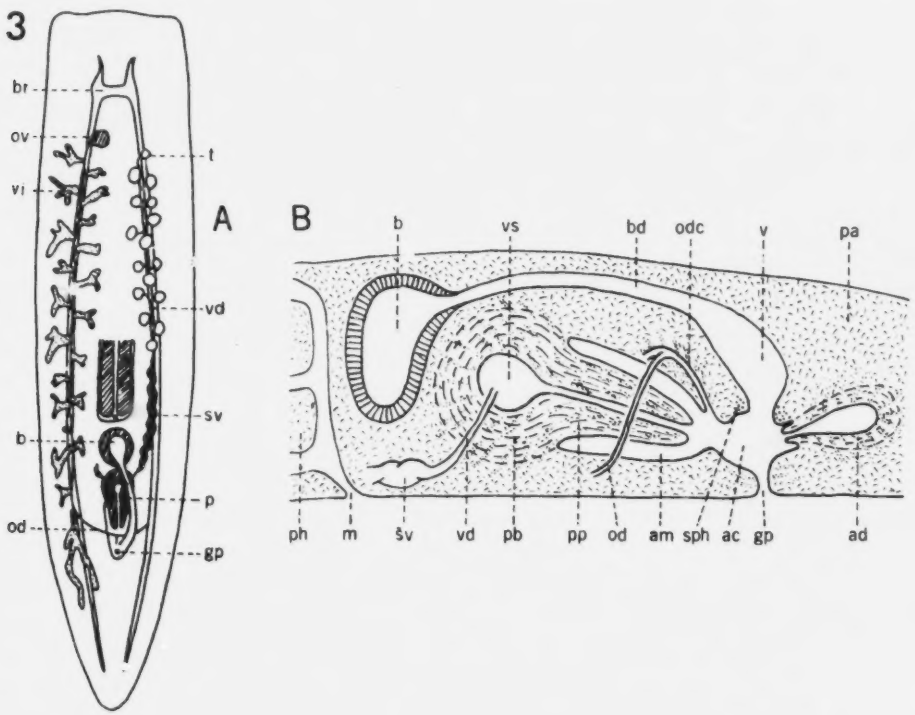

Fig. 3. Reproductive system. A, dorsal view (female gonads indicated on left, male gonads on right side); B, generalized diagram of the copulatory apparatus in sagittal section. ac, common genital atrium; ad, adenodactyl; am, male atrium; b, copulatory bursa; bd, bursal duct; br, brain or cerebral ganglion; gp, gonopore; m, mouth; od, oviduct; odc, common oviduct; ov, ovary; p, penis; pa, parenchyma; pb, penial bulb; ph, pharynx; pp, penis papilla; sph, sphincter; sv, spermiductal vesicle; t, testis; v, vagina; vd, vas deferens; vs, seminal vesicle.

The protonephridial excretory system consists of a network of fine tubes with branches terminating in flame cells and with many pores on the surface of the body.

Muscular fibers are found in several layers underlying the epidermis (integumental muscles), individual fibers traversing the parenchyma in various directions, and variously arranged fibers in the pharynx, the adhesive organ when present, and in parts of the reproductive system.

No separate circulatory system is developed, its functions being taken over by the gastrovascular cavity and the system of interstitial spaces of the parenchyma.

The parenchyma contains the cell bodies of many unicellular glands, the ducts of which open through the epidermis to the outside, through the surface of the adhesive organ, the tip of the pharynx, and various parts of the reproductive organs.

The taxonomically most important structures are those of the reproductive system. All freshwater planarians are hermaphroditic, both male and female genital organs developing in the same individual (Fig. 3). The paired ovaries or germaries (ov) lie in the anterior portion of the body adjacent to the ventral nerve cord. From each ovary originates a canal, the oviduct or ovovitelline duct (od) which proceeds posteriorly along the dorsal side of the nerve cord. At the boundary between the ovary and the oviduct is a small enlargement of the canal, the seminal receptacle. Many vitellaria or yolk glands (vi) branch out from the oviduct, consisting of large eosinophilic cells with yolk inclusions. Cell masses, representing a transition between oogonia and yolk cells, may be attached to the ovaries, forming the so-called parovaria.

The male gonads are numerous testicular follicles (t) located on either side in a zone extending from behind the ovaries to the level of the pharynx, the mouth, or almost to the posterior end (exceptionally, the testes may fuse into one elongated organ on either side). Each testis is connected to the sperm duct or vas deferens (vd) by a thin canal, the vas efferens. The sperm ducts run posteriorly parallel to the nerve cords. In the region of the pharynx they usually widen, forming twisted enlargements filled with sperm, the false seminal vesicles or spermiductal vesicles (sv).

Behind the pharynx is the copulatory apparatus or complex consisting of the terminal portions of the gonoducts and various accessory structures. The genital aperture (gp) leads into a cavity, the genital atrium or antrum, which may be subdivided into several parts separated by strictures: a male atrium (am) enclosing the penial papilla, a female atrium receiving the openings of parts of the female complex, and a common atrium (ac) which connects with the gonopore. The nomenclature of the atria is frequently inconsistent, as the mouth of the oviduct may be in the posterior part of the "male" atrium.

The male copulatory organ or penis is a muscular organ consisting of two parts, the anterior penis bulb (pb) embedded in the parenchyma and the penis papilla (pp) protruding into the male atrium. Generally the two sperm ducts (vd) enter the penis bulb, separately or combined as a common vas deferens, and open into a cavity, the seminal vesicle (vs) or bulbar cavity. From this cavity a narrower duct proceeds into the penis papilla, the ejaculatory duct (de). There are, however, several modifications of this plan found in the different species.

The oviducts or ovovitelline ducts usually approach the midline above the genital atrium and unite to form a common oviduct (odc) which generally opens into the atrium from the dorsal side. A usually sac-shaped accessory organ, the copulatory bursa (b), lies in the space between the pharyngeal pouch and the penis bulb and is connected to the atrium by a muscular tube, the bursal duct or canal (bd), running dorsal to the atrium either in the midline or to one side of it. In a few species the bursa is absent but the bursal canal is developed, either ending blindly or connecting with a branch of the intestine. In the genera *Cura* and *Dugesia*, the paired or united oviducts open into the distal part of the bursal canal instead of the atrium.

Species of the genus *Planaria* have a hollow very muscular organ attached to the posterior portion of the copulatory complex, the adenodactyl (ad) or musculo-glandular organ.

Gland ducts originating in the surrounding parenchyma open into various parts of the copulatory complex: the penial cavity, the terminal parts of the oviducts ("shell glands", sg), the common atrium (cement glands), the adenodactyl, etc.

REPRODUCTION

Reproduction of planarians is either sexual or asexual. Sexual reproduction usually involves copulation of two individuals during which the sperm of one partner are deposited in the copulatory bursa of the other (autofecundation has been observed only in *Cura foremanii* among the American planarians). From the bursa the sperm are expelled through the bursal duct, enter the oviducts, and are finally stored in the seminal receptacles. The ova are fertilized as they pass through the receptacles on their way to the atrium where they accumulate. They are deposited in a cocoon, a rather large (diameter 0.5 to over 3 mm) spherical or ellipsoidal capsule with a shell of horny consistency, attached to the substrate by a gelatinous secretion or, more rarely, by a thin stalk (Fig. 4).

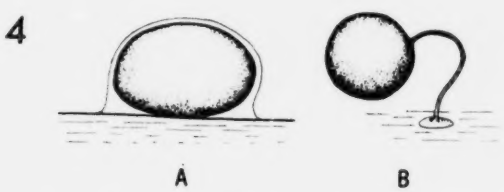

Fig. 4. Egg capsules of planarians. A, unstalked cocoon; B, stalked cocoon.

Each capsule contains several (2-20, sometimes more) zygotes and thousands of yolk cells which serve as food for the developing embryos. When the young hatch from the cocoon one to several weeks after its deposition, they have more or less the shape of the adults, without passing through a larval stage and metamorphosis. They lack, however, any trace of the reproductive system which will develop only when they are almost fully grown.

Asexual reproduction is by fission or by fragmentation. Fission occurs usually at a postpharyngeal level and consists of a tearing apart of the posterior portion of the body. Both parts then regenerate the missing organs, the anterior part a new tail and the posterior part a new head, pharynx, etc. In fragmentation the body breaks up into several smaller portions each of which then encysts, i.e., acquires a rounded shape and encloses itself in a layer of transparent slime which usually adheres to the substrate. After a certain rest period small planarians hatch from the cysts, resembling the young hatched from an egg capsule. Asexual reproduction is very common in some species, and certain populations have been cultured through several generations without developing sexual structures.

CHARACTERS USED IN THE IDENTIFICATION OF PLANARIANS

It is not always possible to identify individual species and even genera by their external characteristics, and the final decision must often be made by examining anatomical features. In a well-explored geographic region one may be reasonably sure to recognize certain species which bear distinctive characters and are known to occur locally, but it is always advisable to have the identification confirmed by anatomical study.

Of the external features, the shape of the anterior end of the quietly gliding animal is often characteristic. It may be pointed (triangular), truncate, or rounded. The lateral edges may protrude as auricular appendages. There may or may not be a constriction or neck behind the head. An adhesive organ may be developed on the frontal margin. The number and arrangement of the eyes sometimes furnish useful specific characters. It is best to prepare an outline sketch of the anterior end of the specimens in gliding motion.

The pigmentation of the body, including both shade and pattern on the dorsal and ventral surfaces, should be noted. The pigments are either granular, enclosed in subepidermal pigment cells, or nongranular and diffused in various tissues. Granular pigments can usually be recognized in microscopical sections, while diffused pigments easily bleach in the reagents used for fixing and storing. Thus, some pigmented planarians have been described from preserved specimens as "white" (e.g., the dark *Dendrocoelopsis vaginata* and the pink *Macrocotyla glandulosa*). In life unpigmented planarians may appear colored from the contents of the intestine visible through the body wall. In this case, however, the areas not penetrated by the intestine and its branches are white: head, body margins, and spots above the pharynx and copulatory complex.

Some anatomical features may be examined on living specimens in squash preparations or on preserved specimens after clearing the tissues or in whole mounts. Detailed studies of the anatomy, however, demand the preparation of serial sections. The characters most frequently used are the structure of the adhesive organ; the configuration of the lateral edge of the body (development of a distinct marginal zone with special differentiations of glands and rhabdites); and an analysis of the reproductive system. The posterior limits of the bands of testes should be determined as well as their location close to the dorsal or to the ventral side. In the structure of the copulatory organs, the size and shape of the penis and the course of the sperm ducts are important. The oviducts may open into the atrium or into the bursal duct. Special sphincters may be developed on the terminal part of the bursal canal or in other places. Further details concerning the copulatory complex are discussed in the descriptions of the individual species.

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SECTION II

KEY TO THE GENERA OF NORTH AMERICAN FRESHWATER TRICLADS

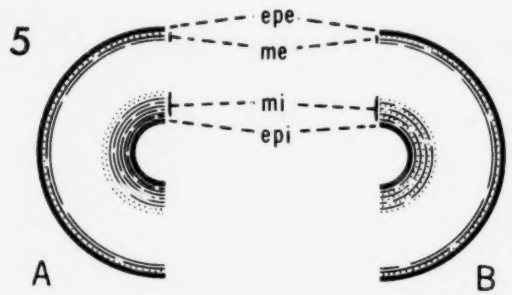

Fig. 5. Muscle layers of pharynx in cross section. A, Planariidae; B, Dendrocoelidae. epe, external epithelium; epi, internal epithelium; me, external muscle layer; mi, internal muscle layer.

1 Internal muscle zone of pharynx consists of two distinct layers, a circular and a longitudinal one (Fig. 5A): Family Planariidae 2
Internal muscle zone of pharynx consists of one layer of intermingled circular and longitudinal fibers (Fig. 5B): Family Dendrocoelidae 9

2 (1) Oviducts, separate or united, open into end part of bursa stalk 3
Oviducts unite, the common oviduct opening into the genital atrium 4

3 (2) Zone of testes extends to level of pharynx: ..... *Cura*
Zone of testes extends to posterior end: ..... *Dugesia*

4 (2) Eyes numerous, forming a band around anterior end: .. *Polycelis*
Eyes two or wanting, if numerous not on head margin 5

5 (4) Adenodactyl present ..... *Planaria*
No adenodactyl 6

6 (5) Anterior end with adhesive organ: 7
Anterior end without adhesive organ: 8

7 (6) Body elongated, flat, with well-developed postpharyngeal region: ..... *Sphalloplana*
Body turtle-shaped, with reduced postpharyngeal region: *Kenkia*

8 (6) Penis normal, with bulb and papilla: ..... *Phagocata*
Penis without bulb, papilla rudimentary: ..... *Hymanella*

9 (1) Anterior end with deeply invaginated adhesive organ: *Macrocotyla*
Anterior end with adhesive disc or without adhesive organ .. 10

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10 (9) Penis with bulb and papilla 11
Penis with large bulb, no papilla: ..... *Rectocephala*

11 (10) Penis bulb rounded, containing seminal vesicle:
Dendrocoelopsis
Penis bulb elongated, containing a prostatic vesicle (Fig.89):
Procotyla

SECTION III

KEY TO THE SPECIES OF NORTH AMERICAN FRESHWATER TRICLADS

1 Anterior end triangular 2
Anterior end truncate 7
Anterior end rounded 35

2 (1) Head rather acutely pointed, with prominent auricles, pharynx pigmented 3
Head bluntly pointed, auricles absent or rounded, pharynx unpigmented 5

3 (2) Auricles long and pointed, ventral side pigmented 4
Auricles short, ventral side usually unpigmented:
Dugesia tigrina (p. 20)

4 (3) No diverticula on ejaculatory duct: *Dugesia dorotocephala* (p. 22)
Ejaculatory duct with a pair of diverticula:
Dugesia antillana (p. 23)

5 (2) Auricles rounded, penis with rounded bulb and a single seminal vesicle, bursal sac absent ..... *Cura foremanii* (p. 19)
Auricles absent, bursal sac developed 6

6 (5) Penis with divided bulb and two seminal vesicles:
Dugesia polychroa (p. 24)
Penis without bulb, with rudimentary papilla:
Hymanella retenuova (p. 31)

7 (1) Frontal margin without adhesive organ 8
Frontal margin with adhesive organ 28

8 (7) Body pigmented 9
Body without pigment, white 21

9 (8) Eyes normally two (with occasional accessory eye spots), close together 10
Eyes numerous, on margin of head (genus *Polycelis*) 19

10 (9) Pharynx single (monopharyngeal) 11
Pharynges multiple (polypharyngeal) 18

11 (10) Adenodactyl present 12
No adenodactyl present 13

12 (11) External muscle layer of penis papilla thickened, adenodactyl opens into a separate chamber of the genital atrium:
Planaria dactyligera musculosa (p. 29)
External muscle layer of penis papilla not thickened, adenodactyl opens intc atrium near gonopore:
Planaria dactyligera dactyligera (p. 28)

13 (11) Penis papilla with terminal lobe, ejaculatory duct opening on ventral side of papilla .... *Phagocata crenophila* (p. 39)
Penis papilla without terminal lobe, ejaculatory duct opening at tip of papilla 14

14 (13) Penis rudimentary, without bulb and with small papilla: *Hymanella retenuova* (p. 31)
Penis well-developed, with bulb and papilla 15

15 (14) Ejaculatory duct with blind diverticulum: *Phagocata velata* (p. 35)
Ejaculatory duct without diverticulum 16

16 (15) Copulatory bursa rounded, sac-shaped 17
Copulatory bursa U-shaped, testes in part longitudinally fused ..... *Phagocata vernalis* (p. 34)

17 (16) Penis with round bulb and narrow ejaculatory duct: *Phagocata bulbosa* (p. 36)
Penis with small bulb and wide undivided penial lumen: *Phagocata monopharyngea* (p. 33)

18 (10) Penis papilla long, conical, with fibrous layer below outer epithelium, penis lumen with two seminal vesicles: *Phagocata gracilis* (p. 43)
Penis papilla short, truncate, with intermingled circular and longitudinal muscle fibers below outer epithelium, penis lumen not subdivided .... *Phagocata woodworthi* (p. 44)

19 (9) Bursa duct with anterior glandular and posterior non-glandular sections 20
Bursa duct non-glandular throughout: *Polycelis coronata borealis* (p. 27)

20 (19) Penis papilla as large as, or larger than, penis bulb: *Polycelis coronata coronata* (p. 25)
Penis papilla smaller than penis bulb: *Polycelis coronata brevipenis* (p. 26)

21 (8) Head with slender, pointed auricles: *Phagocata bursaperforata* (p. 37)
Head without pointed auricles 22

22 (21) Polypharyngeal ..... *Phagocata gracilis* (p. 43)
Monopharyngeal 23

23 (22) Eyes normally two (smaller accessory eye spots may occur) .. 24
Eyes wanting ..... *Procotyla typhlops* (p. 64)
Eyes many, in two longitudinal rows: *Phagocata morgani polycelis* (p. 41)

24 (23) Eyes separated by about 1/3 the width of the head, about equidistant from frontal and lateral margins: *Dendrocoelopsis alaskensis* (p. 60)
Eyes close together, removed farther from frontal than from lateral margins 25

25 (24) Anterior intestinal ramus extending to a level in front of the eyes ..... *Planaria occulta* (p. 30)
Anterior intestinal ramus starts behind level of eyes 26

26 (25) Opening of ejaculatory duct at tip of penis papilla: *Phagocata oregonensis* (p. 32)
Opening of ejaculatory duct on ventral side of penis papilla 27

27 (26) Tip of penis papilla with a muscular, wart-like structure, testes extend to level of mouth: *Phagocata morgani morgani* (p. 40)
Tip of penis papilla without muscular wart, testes extend to posterior end ..... *Phagocata nivea* (p. 42)

28 (7) Inner pharyngeal muscle zone with separate layers of circular and longitudinal fibers 29
Inner pharyngeal muscle zone with one layer of intermingled circular and longitudinal fibers 30

29 (28) Body turtle-shaped, with cylindrical snout, postpharyngeal region reduced ..... *Kenkia rhynchida* (p. 56)
Body elongated, flat, in life without snoutlike extension, postpharyngeal region well-developed: genus *Sphalloplana* (The systematics of this genus is undergoing great changes as more material is made available to specialists by the efforts of speleological investigators. For in part unreliable data on individual species see the descriptive part of the report, pages 45-55.)

30 (28) Adhesive organ forms a deep subterminal invagination on the head, copulatory complex excessively glandular: *Macrocotyla glandulosa* (p. 57)
Adhesive organ in form of a disc or shallow depression 31

31 (30) Body pigmented 32
Body unpigmented, white 34

32 (31) Penis with voluminous bulb, no papilla: *Rectocephala exotica* (p. 65)
Penis with normal bulb and papilla 33

33 (32) Testes ventral, to level of gonopore: *Dendrocoelopsis vaginata* (p. 58)
Testes dorsal, to posterior end: *Dendrocoelopsis piriformis* (p. 59)

34 (31) Eyes wanting ..... *Dendrocoelopsis hymanae* (p. 61)
Eyes two, or two groups of scattered eyes:
Procotyla fluviatilis (p. 63)
Eyes multiple, arranged in two longitudinal rows:
Dendrocoelopsis americana (p. 62)

35 (1) Penis reduced, without bulb and with rudimentary papilla:
Hymanella retenuova (p. 31)
Penis normal, with bulb and papilla 36

36 (35) Ventral surface unpigmented ..... *Phagocata tahoena* (p. 38)
Ventral surface pigmented ..... *Dugesia polychroa* (p. 24)

SECTION IV

SPECIES CHARACTERISTICS AND RANGES

Cura foremanii (Girard, 1852)

Synonyms: *Dugesia foremanii* Girard, 1852; *Planaria foremanii*: Stimpson, 1857; *P. simplissima* Curtis, 1900; *P. simplicissima*: Morgan, 1904; *P. lugubris*: Morgan, 1901 (not O. Schmidt, 1861); *Curtisia simplicissima*: Graff, 1916; *C. foremani*: Kenk, 1930; ?*Planaria gonocephala*: Pearl, 1903 (not Dugès, 1830); ?*Dugesia modesta* Girard, 1893.

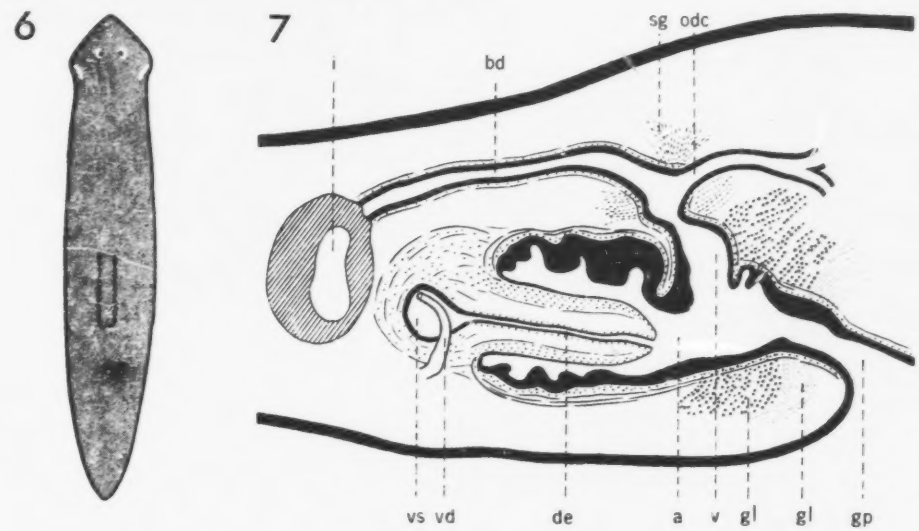

Fig. 7 after Kenk (1935).

Length 7-15 mm, generally rather broad and thick. Head bluntly triangular, with rounded, only slightly protruding auricles. Color uniformly gray or brown to almost black, ventrally lighter. Besides the (normally two) white eye fields there is a light oblique dash on the dorsal side of each auricle and the mouth and gonopore appear as white spots. Pharynx unpigmented (white), which distinguishes the species from the common American species of *Dugesia* (this may be checked on the freshly extirpated pharynx). Testes very few, dorsal, between ovaries and level of mouth. Penis relatively small, with moderately developed bulb containing the rounded seminal vesicle and a finger-shaped papilla traversed by a straight ejaculatory duct opening at its tip. No bursal sac is developed, the bursal canal attaches to a branch of the intestine. The two oviducts unite behind the copulatory apparatus and open into the bursal duct which also receives the shell glands. Cocoon spherical, attached to substrate by a thin, flexible stalk. Inhabitant of cool streams. Reproduces only sexually. Eastern half of North America, from New Brunswick to Louisiana and westward to Minnesota and Arkansas. Principal literature: Curtis (1900), Stevens (1904), Kenk (1935 and 1944).

Dugesia tigrina (Girard, 1850)

Synonyms: *Planaria maculata* Leidy, 1847; *P. tigrina* Girard, 1850; *P. lata* Sivickis, 1923; *Dugesia maculata*: Girard, 1851; *D. lata*: Hyman, 1951; *Euplanaria maculata*: Kenk, 1930; *E. lata*: Kenk, 1930; *E. tigrina*: Kenk, 1935; *E. novangliae* Hyman, 1931; *?E. microbursalis* Hyman, 1931; *?Dugesia microbursalis*: Hyman, 1939; *?D. gonocephaloides* Girard, 1850; *?Planaria gonocephaloides*: Stimpson, 1857; *?P. gonocephala*: Woodworth, 1897 (not Dugès, 1830).

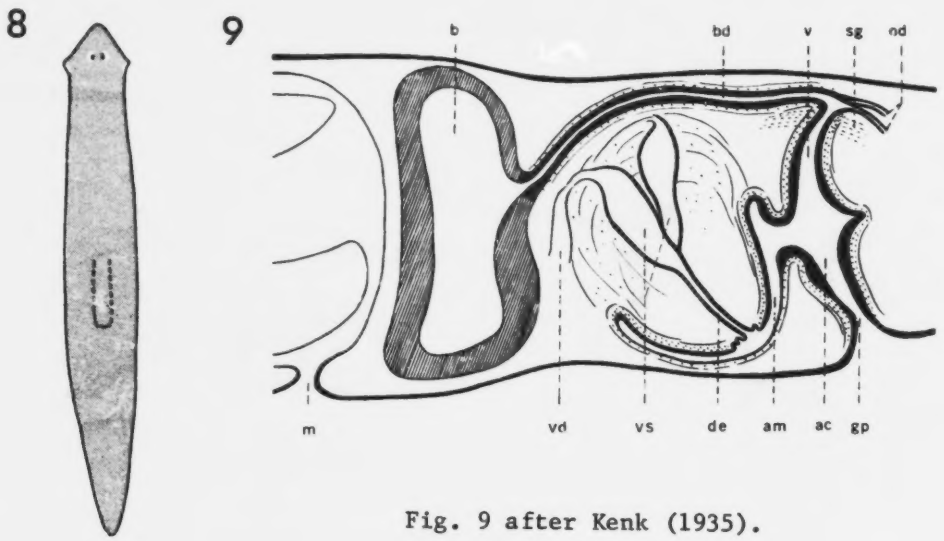

Fig. 9 after Kenk (1935).

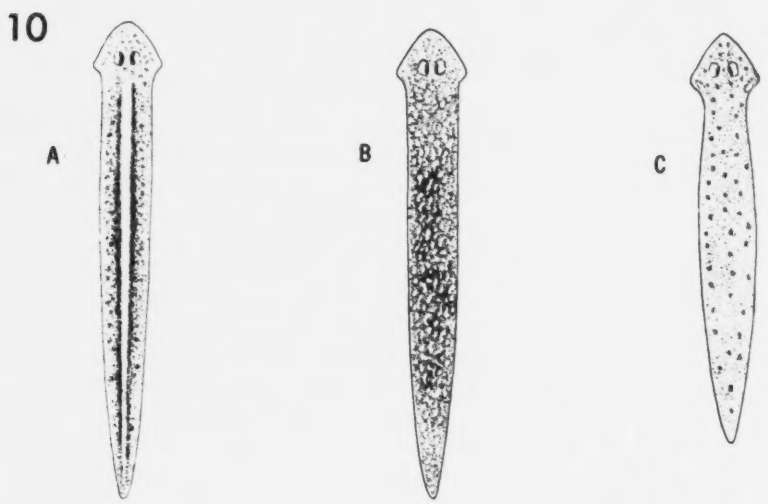

Fig. 10. Pigment patterns (after Hyman, 1939b).

A very common species, widely distributed and polytypic. Mature animals 6-18 mm long and 1-3 mm wide. Head triangular, with bluntly pointed or somewhat rounded anterior tip. Auricles short and broad. Eyes normally two, situated close together, anterior to the level of the auricles. Coloration very variable, sometimes appearing almost uniformly brown to the naked eye or composed of spots of various shades of brown with irregularly dispersed white splotches (spotted type); or showing a pair of dark longitudinal stripes separated by a light middorsal streak (striped type), both types sometimes occurring in the same population. Ventral surface usually unpigmented. Pharynx pigmented, with white tip. Anatomically very similar to *D. dorotocephala*. Testes ventral, reaching close to posterior end. Penis with round bulb and short conical papilla directed posteroventrally. The vasa deferentia ascend to the dorsal side before entering the bulb, then curve posteroventrally, each widening into an elongated seminal vesicle. They unite at the base of the papilla and proceed to its tip as a narrower ejaculatory duct. Occasionally the lumen of the penis is expanded as a single seminal vesicle, apparently a transitory condition. Bursal duct forms a rather sharp angle at the entrance of the separate or united oviducts. Shell glands open into the bursal duct below the mouths of the oviducts. The small common genital atrium frequently shows a posterior diverticulum. Reproduction sexual and asexual. Cocoon round, stalked. Widely distributed, generally in warm ponds, lakes, and rivers in the United States and southern Canada, from the Atlantic to the Pacific coasts. Principal literature: Curtis (1902), Sivickis (1923), Hyman (1939b), Kenk (1935, 1944).

Dugesia dorotocephala (Woodworth, 1897)

Synonyms: *Planaria dorotocephala* Woodworth, 1897; *P. agilis* Stringer, 1909; *Euplanaria dorotocephala*: Kenk, 1930; *E. agilis*: Kenk, 1930; *E. philadelphica* Hyman, 1931; *Dugesia agilis*: Hyman, 1939; *D. diabolis* Hyman, 1956.

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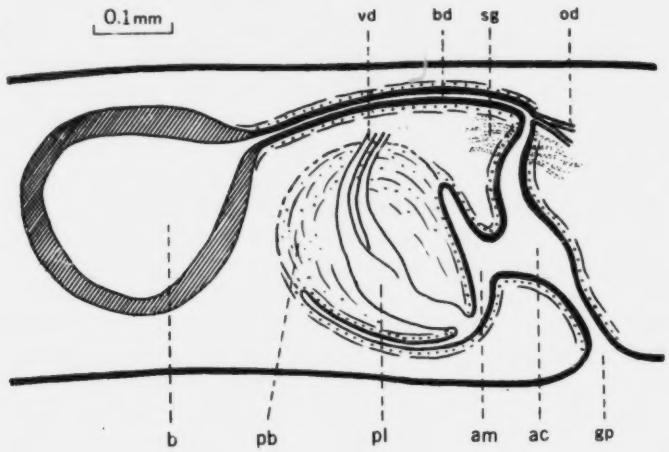
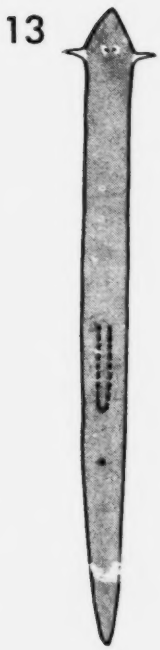


A polytypic species, in nature up to 30 mm long and about 3.5 mm wide (may grow larger in laboratory cultures). Head triangular, with slightly convex sides and rather pointed tip. A pair of elongated, sharply pointed auricles extends laterally, during gliding usually held elevated. Eyes normally two, close together, just anterior to the base of the auricles. Color brown to almost black dorsally, somewhat lighter ventrally, occasionally with a darker middorsal streak behind the pharynx. Under magnification small white and dark spots are seen on the general background color. Pharynx pigmented light gray, with a short white tip. Testes numerous, ventral, extending to posterior end. Penis with spherical bulb and short conical or rounded papilla pointing posteroventrally. Vasa deferentia enter bulb dorsolaterally, bend down toward the axis of the papilla, and increase in diameter, each duct forming a seminal vesicle. Distally they unite to a short ejaculatory duct opening at the tip of the papilla. Under certain conditions the two seminal vesicles may appear fused, forming a larger, round vesicle. Bursal duct running posteriorly above the penis, then curving ventrally toward the small common atrium. At the turning point it receives the two oviducts from the posterolateral sides. Below these openings (which are close together) is a short zone where numerous outlets of shell glands open into the bursal canal (none into the oviducts). Sexual or asexual reproduction may predominate in different populations. Cocoon spherical, stalked. Distributed in running and standing waters across the continent in the United States and southern Canada. Principal literature: Woodworth (1897), Hyman (1925, 1929, 1931b), Kenk (1944).

Dugesia antillana Kenk, 1941



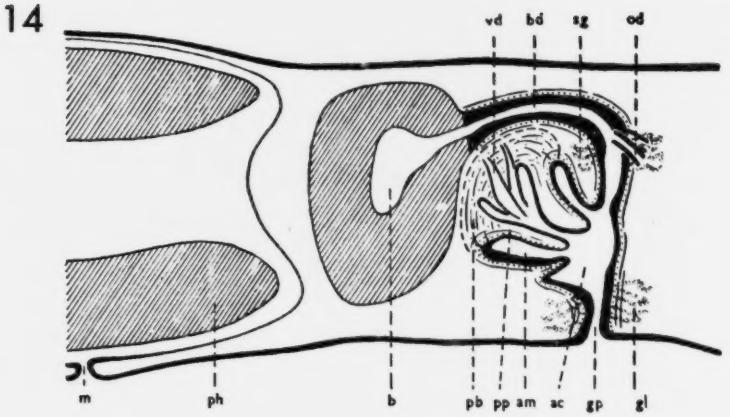


Fig. 14 after Kenk (1941).

Very slender, up to 19 mm long and 0.7 mm wide. Head triangular, rather broad, with long, pointed auricles. Dorsal side grayish-brown, sometimes with an indistinct darker streak in the prepharyngeal midline, ventrally somewhat lighter. Eyes usually two, lying close together. The two eye fields, the auricles and a spot at the site of the gonopore lack pigment. Pharynx pigmented. Testes numerous, predominantly dorsal, starting behind the ovaries and extending to near the posterior end. At full maturity, some testes may occupy the entire dorsoventral diameter. Vasa deferentia expand at the level of the mouth into spermiductal vesicles, then narrow again as they approach the penis. The gonopore leads into a common atrium which dorsally receives the bursal duct and anteriorly connects with the male atrium. Penis with rather small bulb and short, conical papilla. The vasa deferentia enter the bulb dorsolaterally and widen within the bulb into a pair of spindle-shaped cavities which unite in the papilla to a short canal, the ejaculatory duct, which opens at the tip of the papilla. Close to the union of the two sperm ducts, a pair of tubular diverticula extend toward the penial bulb (very characteristic of the species). Copulatory bursa voluminous, bursal stalk running dorsal to the penis and bending ventrally behind it to approach the common atrium. Oviducts open separately into the bursa stalk. Below their opening, the stalk receives numerous eosinophilic shell glands. Inhabits mountain streams. Only sexual reproduction has been observed. Known only from Puerto Rico. Literature: Kenk (1941).

Dugesia polychroa (O. Schmidt, 1861)

Synonyms: *Planaria polychroa* O Schmidt, 1861; *P. lugubris*: Böhmig, 1909; *Dugesia lugubris*: Ball, 1969 (in part).

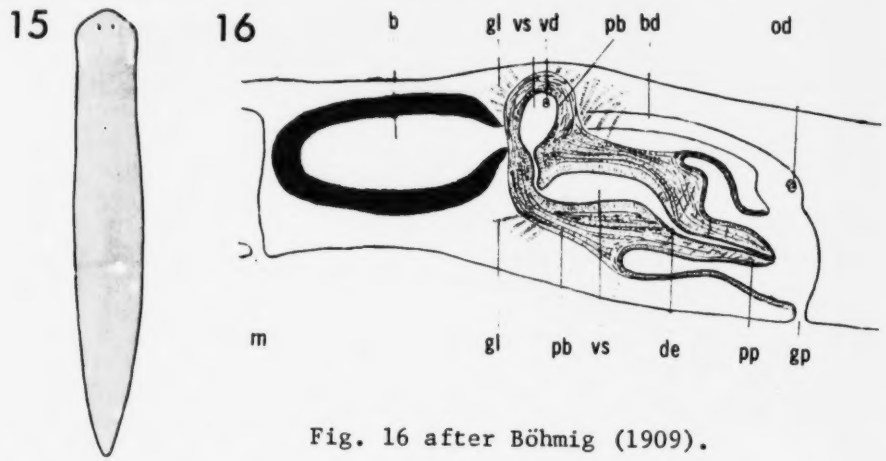


Fig. 16 after Böhmig (1909).

Mature specimens up to 20 mm long and about 3 mm wide. Head more or less rounded, occasionally showing a small median projection. A gentle narrowing or neck behind the lateral edges. Eyes usually two, close to the frontal end. Color variable, usually a shade of brown, either uniformly distributed or somewhat spotty. A pair of lighter elongated auricular sense organs is seen near the lateral margin of the head some distance behind the eye level. Pharynx unpigmented. Testes numerous, dorsal, extending to posterior end. The penis consists of a very muscular bulb and a generally conical papilla. The bulb is divided into two sections, an anterodorsal part which contains the rounded anterior seminal vesicle and a posterior part enclosing the elongated posterior seminal vesicle. The two vesicles are joined by a narrower canal. From the posterior vesicle the ejaculatory duct proceeds through the papilla to its tip. The vasa deferentia open separately into the anterior seminal vesicle, the two oviducts into the posterior part of the bursa stalk. Reproduction only sexual. Cocoon spherical, stalked. This species, widely distributed in Europe, has been introduced to the St. Lawrence River system in eastern Canada (Ontario) and New York State. Principal literature: Böhmig (1909), Komárek (1925), Ball (1969), Reynoldson and Bellamy (1970).

Polycelis coronata coronata (Girard, 1891)

Synonym: *Phagocata coronata* Girard, 1891.

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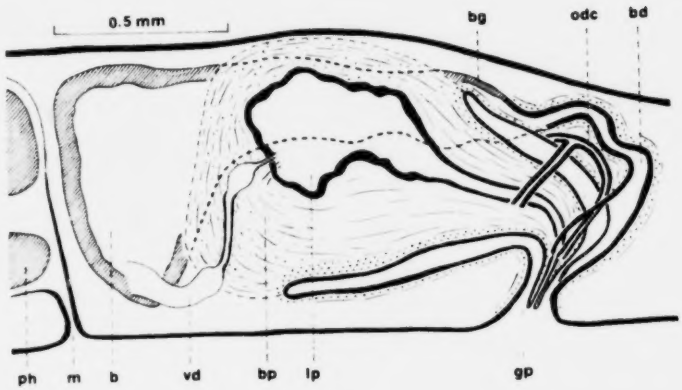

Mature animals up to 19 mm long and 2.4 mm wide. Head truncate, with convex frontal margin and a pair of triangular auricles with rounded tips extending anterolaterally. Eyes multiple, irregularly scattered on the dorsal side of the head in a band which parallels the margin of the head, narrows posteriorly, and extends over the anterior quarter of the prepharyngeal region. Dorsal side brown to almost black, ventral side lighter. The individual eyes have no pigmentless fields. Testes ventral, prepharyngeal. Penis with very muscular bulb and more or less conical papilla, the size relations of the two parts being subject to great variation according to the state of contraction of the organ (generally the papilla is as long as the bulb). The male atrium duplicates in shape the penis papilla and receives in its posterior part the mouth of the common oviduct. Bursa usually large, with a wide bursal duct proceeding backward to one side (usually left) of the midline, lined with the same glandular epithelium as the bursal sac and covered by a very feeble muscle layer. Only in its posterior fourth the histological aspect of the epithelial lining changes suddenly, the canal narrows, and its muscular coat thickens. Reproduction sexual and asexual. Inhabits springs and cold creeks in southern Wyoming, Utah, Montana, New Mexico. Principal literature: Girard (1893), Braithwaite (1962).

Polycelis coronata brevipenis new subspecies

Synonym: *Polycelis coronata:* Hyman, 1931.

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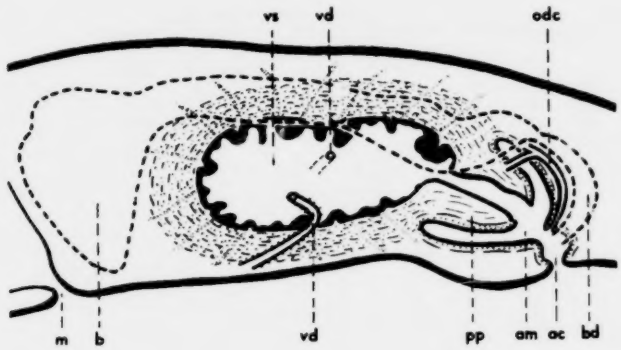

Fig. 19 after Kenk (1952).

Externally indistinguishable from the subspecies *coronata*, differing from it chiefly in the anatomy of the copulatory apparatus. 13-20 mm long when mature. The penis bulb is very large and elongated, the penis papilla short, plug-like. The penial cavity or seminal vesicle is voluminous, stretched out in the longitudinal axis, and receives the two sperm ducts laterally, often asymmetrically. The ejaculatory duct is rather wide and short. The bursal canal, which lies on the left side of the penis, has a wide anterior portion which is lined with a glandular epithelium similar to that lining the bursal sac. Where the duct turns downward at the level of the male atrium, its histological nature changes abruptly. The epithelium becomes nonglandular and the duct acquires a strong muscle coat (this division of the bursal duct into an anterior glandular and a posterior muscular part is seen also in the subspecies *coronata* but not in *borealis*). Reproduction sexual and by fission. Reported from South Dakota and Colorado, but is probably more widely distributed. Literature: Hyman (1931a), Kenk (1952).

Polycelis coronata borealis Kenk, 1953

Synonym: *Polycelis borealis* Kenk, 1953.

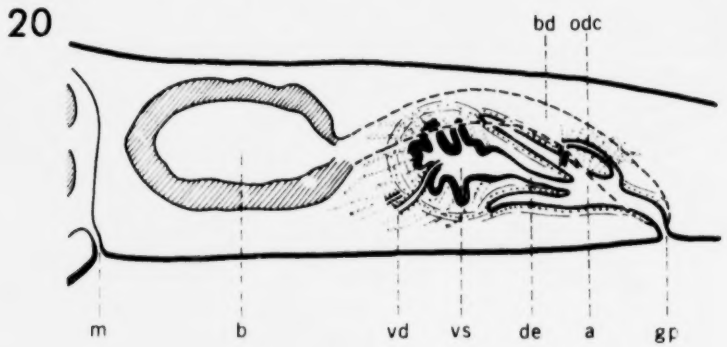

Fig. 20 after Kenk (1953).

Not distinguishable from the nominate subspecies by external features. Up to 20 mm long and 2.5 mm wide. Differs from the subspecies *coronata* and *brevipenis* by the anatomy of the bursal duct which is evenly muscular throughout its length and is not divided into glandular and muscular sections. The penis has a well-developed, conical papilla (in *brevipenis* the papilla is reduced in size, blunt, containing a short ejaculatory duct). Reproduction sexual and asexual. In springs, cold streams, also in mountain lakes, Alaska, northern Wyoming, Idaho. Principal literature: Kenk (1953).

Planaria dactyligera dactyligera Kenk, 1935

Synonym: *Planaria dactyligera* Kenk, 1935.

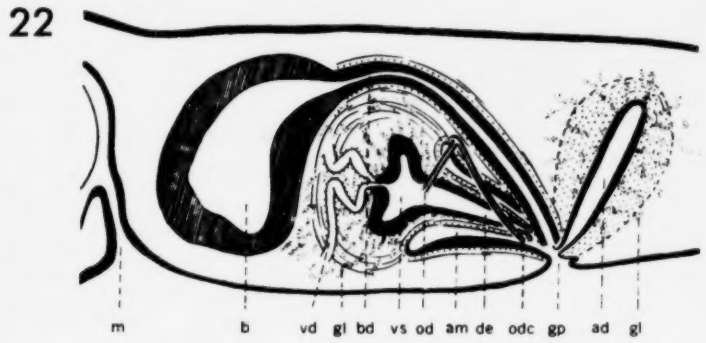

Fig. 22 after Kenk (1935).

Length of mature animals up to 13 mm, width 1.75 mm. Head truncate, with almost straight frontal margin and rounded lateral edges. Behind the head is an insignificant narrowing or neck. Eyes usually two, their distance from each other about 1/3 the width of the head and their distance from the frontal margin much greater than from the lateral margins. Dorsal side darkly pigmented, gray, brown, or black; ventral surface lighter. Externally indistinguishable from *Hymanella* and some species of *Phagocata*. Testes predominantly ventral, their zone on either side reaching to the level of the mouth. The gonopore leads into the genital atrium which has only one compartment, the male atrium, as the openings of the common oviduct, the bursal canal, and the adenodactyl are in the immediate vicinity of the gonopore. The sperm ducts enter the penis bulb anterolaterally and open into the seminal vesicle with a common opening. The ejaculatory duct emerging from the vesicle tapers posteriorly and open at the tip of the penis papilla. The thickness of the muscle coat underlying the outer epithelium of the papilla is about equal to that adjoining the epithelium of the male atrium. Behind the gonopore is the hollow adenodactyl. Cocoon ellipsoidal or spherical, unstalked. Only sexual reproduction has been observed. Inhabitant of springs and creeks in Virginia. Literature: Kenk (1935).

Planaria dactyligera musculosa Kenk, 1969

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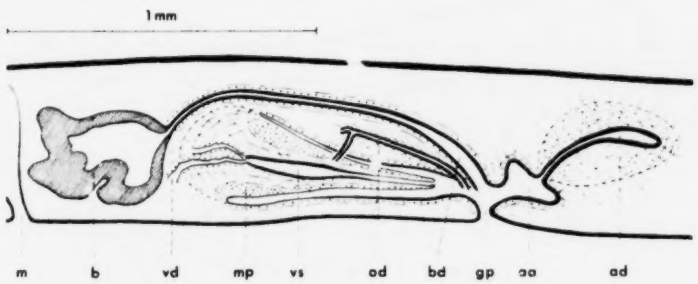

Fig. 23 after Kenk (1969).

Differs from the subspecies *dactyligera* mainly in the anatomy of the penis and of the genital atrium. The outer muscle zone of the penis papilla (mp) consists of a very thick layer of circular fibers followed by a normal layer of longitudinal muscles. The adenodactyl, instead of having its opening at the gonopore, connects with a separate compartment (aa) of the atrium lying posterior to the genital aperture. In streams and springs, North Carolina, southern Virginia, and Louisiana. Literature: Kenk (1969).

Planaria occulta Kenk, 1969

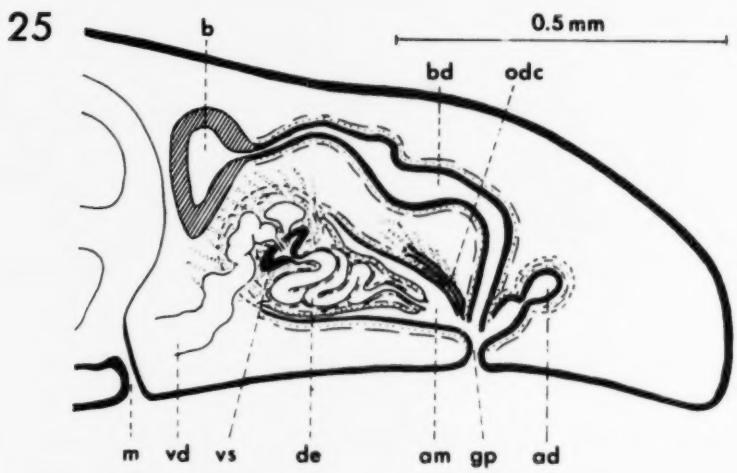

Fig. 25 after Kenk (1969).

A small, white planarian up to 9 mm long and 1.5 mm wide. Head truncated, with slightly convex frontal margin (which, in the gliding animal, may present an indication of a bulge in the center). Eyes two, their distance from each other amounting to 1/4 the width of the head, each eye farther removed from the frontal than from the lateral margin. Externally very similar to the eastern *Phagocata morgani* and the western *P. oregonensis*. However, in *P. occulta* the tip of the anterior intestinal ramus extends between the two eyes whereas in the adult *P. morgani* and *P. oregonensis* its anterior tip is behind the eye level. Testes predominantly ventral, stopping posteriorly at the level of the mouth. Penis with medium large bulb and elongated conical papilla. Vasa deferentia opening independently into a glandular seminal vesicle. The highly convoluted ejaculatory duct ends at the tip of the penial papilla and appears to be capable of eversion. The common oviduct and, behind it, the stalk of the copulatory bursa connect with the genital atrium close to the genital aperture. Posterior to the aperture, the atrium extends into a small compartment which receives the opening of the adenodactyl. This is a hollow organ with a thick and dense muscle shell. The most outstanding characteristics of the species are the structure of the penis and the presence of the adenodactyl. So far found only in a well in the western part of Virginia. Literature: Kenk (1969).

Hymanella retenuova Castle, 1941

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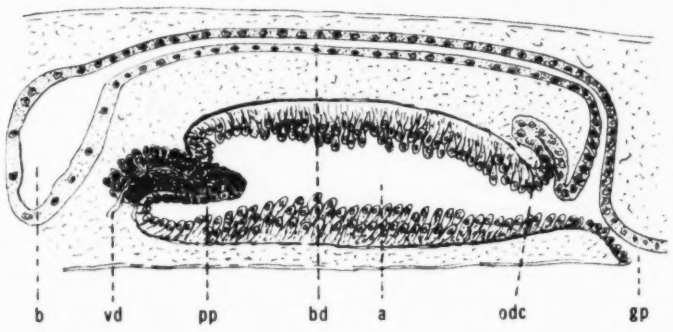

Fig. 27 after Hyman (1955).

Mature animals 7-14 mm long and 1.3-2.5 mm wide. Head of gliding animal truncate with bulging frontal margin, at times appearing low triangular. Lateral corners of head rounded, no distinct necklike constriction behind them. Eyes two, farther removed from front end than from lateral margins. Pigmentation grayish or brown. In life not distinguishable from pigmented species of *Phagocata* or *Planaria*. Testes not well analyzed, possibly dorsolateral and prepharyngeal (or ventral and longitudinally fused?). Vasa deferentia behind the spermiductal vesicles ascend to the penis and unite. Penis very small, without bulb, consisting of a small papilla traversed by the ejaculatory duct formed by the union of the sperm ducts. Genital atrium very large, represented only by the male atrium which at its posterior end receives the opening of the common oviduct from the dorsal side. Copulatory bursa of varying size, its duct rather narrow, running above the atrium and posteriorly arching down to the gonopore. No separate vagina is differentiated. Cocoon ellipsoidal, unstalked, is carried in the atrium up to four weeks before being deposited. In vernal pools and seepage springs, apparently widely distributed in the east of North America, from Massachusetts to North Carolina and Louisiana and west to Ontario. Principal literature: Castle (1941), Hyman (1955).

Phagocata oregonensis Hyman, 1963

Synonym: *Fonticola oregonensis*: Ball, 1969.

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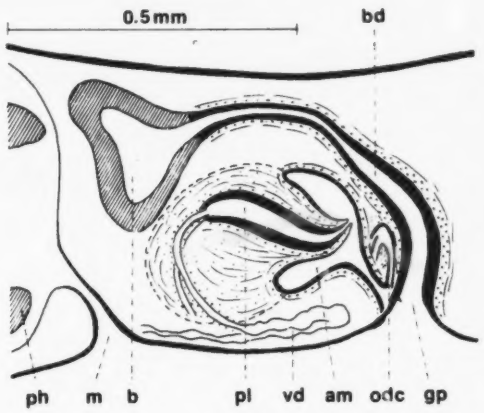

Fig. 29 after Kenk (1970a).

A small, white species up to 8 mm long and 1.5 mm wide. Head truncate, frontal margin with slightly protruding central and lateral portions. Lateral edges rounded, extending laterally, causing a constriction to appear behind the head. Eyes usually two, but smaller supernumerary eye spots are not rare. The distance between the two principal eyes is 1/5 to 1/4 the width of the head at eye level, their distance from the frontal margin greater than from the lateral margins. The tip of the anterior intestinal ramus is behind the level of the eyes. Externally similar to the Alaskan *P. nivea* and the eastern *P. morgani*. Testes ventral, extending posteriorly behind the copulatory complex (in *P. morgani* only to the level of the mouth). Penis consists of a medium size bulb and a short, conical, pointed papilla. The sperm ducts, after expanding at the sides of the pharynx as spermiductal vesicles, continue posteriorly to the level of the male atrium, then turn forward again to enter the penis bulb laterally. They open into the penial lumen independently, without first uniting. The lumen is an elongated cavity, not differentiated into seminal vesicle and ejaculatory duct, and opens at the tip of the penis papilla. The openings of the common oviduct and of the canal of the copulatory bursa are close to the gonopore. No common genital atrium is developed. Known only from a spring in Portland, Oregon. Literature: Hyman (1963), Kenk (1970a).

Phagocata monopharyngea Hyman, 1945

Synonyms: *Phagocata gracilis monopharyngea* Hyman, 1945; *Fonticola gracilis monopharyngea*: Ball, 1969.

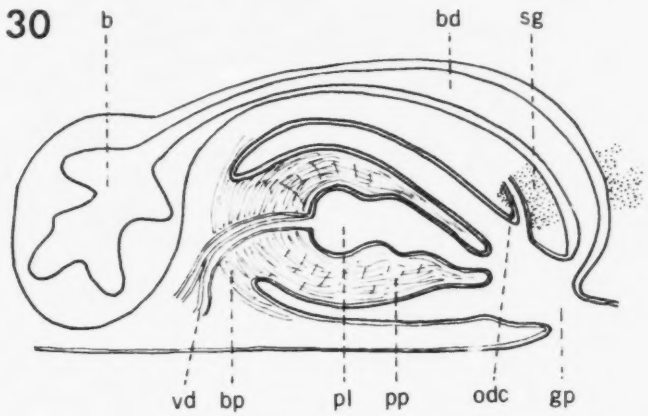

Fig. 30 after Hyman (1945).

A problematic species. Preserved specimens up to 15 mm long, rather broad. Head truncate, with slightly indicated auricles, without adhesive organ. Pigmentation dark gray. Eyes normally two, frequently with small accessory eyes. No testes seen. Penis with small bulb and large, conical papilla. Vasa deferentia enter and traverse the bulb and open separately into the wide elongated penial lumen which is situated in the papilla and extends to its tip. Common oviduct opens into posterodorsal wall of atrium. Copulatory bursa sac-shaped, bursal duct narrow in its anterior part, widens gradually as it proceeds posteriorly to join the common atrium. Known from the outlet of a tile drain, Iowa. Literature: Hyman (1945).

Phagocata vernalis Kenk, 1944

Synonym: *Fonticola vernalis*: Ball, 1969.

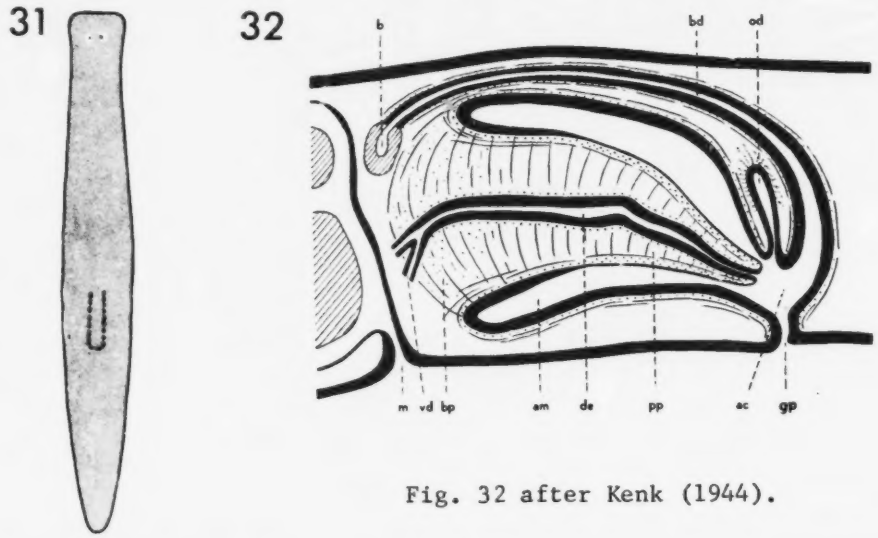

Fig. 32 after Kenk (1944).

Length up to 12 mm, width 1.5 mm. Head truncate, somewhat variable in shape during locomotion. Lateral edges of frontal margin rounded, behind them a very slight narrowing of the lateral margins (neck). Dorsal side gray, often with brownish hue, sometimes with darker longitudinal streaks; ventral surface lighter. Pigment is lacking in the ocular spaces and at the oral and genital apertures. Pigmentation may be almost absent in very young specimens and in animals ready for asexual reproduction. Eyes two, farther removed from the frontal than from the lateral margins. Cannot be distinguished from several other species by external characters. Rarely found sexually mature. Testes few, ventral, prepharyngeal, in part longitudinally fused. Penis with rather small bulb and elongated, conical papilla. Vasa deferentia enter bulb and unite to form a rather narrow longitudinal canal, the ejaculatory duct, opening at the tip of the papilla. No seminal vesicle is developed. Copulatory bursa U-shaped, narrow in the midline, the two horns extending anteroventrally and ending below the intestine. Oviducts unite in the space between the male atrium and the bursal duct and open into the atrium anterior to the mouth of the bursal duct. Reproduction is principally asexual, by fragmentation followed by encystment. Found usually in temporary ponds in winter and early spring. Distributed chiefly in the Mid-West (Michigan, Ontario, probably Illinois and Indiana) and Tennessee. Principal literature: Kenk (1944).

Phagocata velata (Stringer, 1909)

Synonyms: *Planaria velata* Stringer, 1909; *Fonticola velata*: Kenk, 1930.

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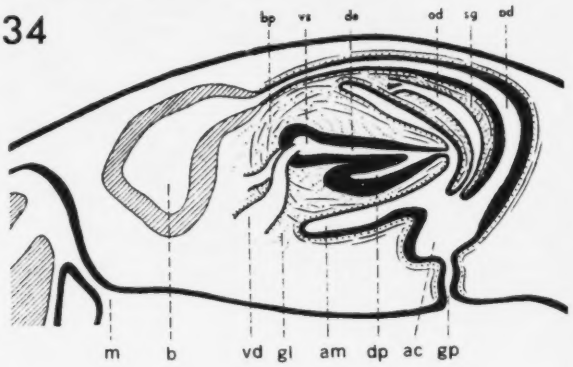

Fig. 34 after Kenk (1944).

Length up to 20 mm, width 2 mm. Head truncated, with slightly convex frontal margin and rounded lateral edges. Behind the head a faint constriction (neck) may occur in gliding locomotion. Dorsal surface usually dark gray to almost black, occasionally with a darker streak along the postpharyngeal midline. Ventral side lighter. Young specimens and individuals before fragmentation may be very lightly pigmented. Eyes usually two, farther distant from the frontal than from the lateral margins. Externally not distinguishable from several other American planariids. Testes numerous, predominantly dorsal, distributed almost to the posterior end. Genital atrium divided into common and male atria. Penis with small bulb and conical papilla. Vasa deferentia enter bulb ventrolaterally and open separately into a bulbar cavity, the seminal vesicle, from which the ejaculatory duct proceeds to the tip of the papilla. Close to its opening, a ventral diverticulum branches off, extending toward the base of the penial papilla. Copulatory bursa sac-shaped, its canal opening into the common atrium. Reproduction sexual or asexual, the latter by fragmentation and encystment. In springs, streams, and spring-fed ponds, apparently all across the continent. Principal literature: Stringer (1909), Castle (1928), Castle and Hyman (1934), Kenk (1944).

Phagocata bulbosa Kenk, 1970a

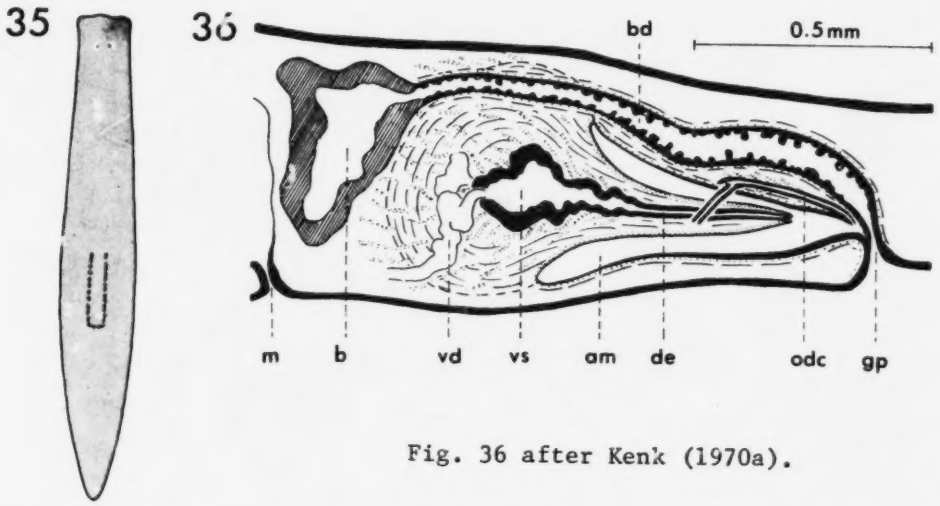

Fig. 36 after Kenk (1970a).

Mature animals up to 12 mm long and 1.7 mm wide. Head truncate, with straight or centrally convex frontal margin and rounded lateral edges. Behind the head is a very slight narrowing of the body. Eyes normally two, rather close together and removed from the anterior end. Dorsal surface uniformly gray or somewhat mottled, ventral side lighter. Cannot be separated by its external features from some other pigmented species of the same genus or from *Planaria dactyligera* and *Hymanella retenuova*. Testes numerous, predominantly ventral, situated on either side in a broad zone extending from behind the ovary to the level of the mouth. There is no common genital atrium developed. Penis with a spherical, muscular bulb and a conical, rather stiff, pointed papilla. Vasa deferentia enter bulb anteroventrally retaining their expanded shape as spermiductal vesicles, form a few convolutions within the bulb, and open separately into the seminal vesicle. This cavity tapers posteriorly to a narrow straight canal, the ejaculatory duct, which opens at the tip of the penial papilla. The openings of the common oviduct and of the bursa stalk are close to the gonopore. Cocoon ellipsoidal, unstalked. Only sexual reproduction observed. In seepage springs, North Carolina. Literature: Kenk (1970a).

Phagocata bursaperforata Darlington, 1959

Synonym: *Fonticola bursaperforata*: Ball, 1969.

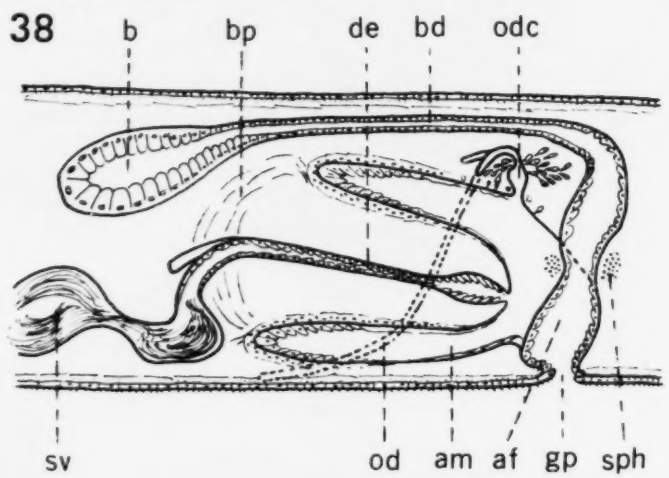

Fig. 37 after Carpenter (1970).
Fig. 38 after Darlington (1959).

A slender species, sexually mature specimens measuring 10-14 mm in length and about 1 mm in width. Head truncate, with slightly convex frontal margin and a pair of rather long, thin, pointed auricles extending anterolaterally, with a slight constriction behind them. Eyeless and unpigmented, white. Pharynx situated rather far back. Testes in moderate number, prepharyngeal, may bridge the entire dorsoventral diameter of the body. Penis consists of a relatively small bulb and a cylindrical papilla tapering toward the tip. The vasa deferentia narrow behind the spermiductal vesicles, enter the penis bulb ventrolaterally, and unite within the bulb to a straight canal, the ejaculatory duct, without passing through an enlarged cavity or seminal vesicle. The duct widens only moderately just before its opening at the tip of the penis papilla. Genital atrium divided into male and female atria. The outlet of the common oviduct is on the dorsal wall of the male atrium, rather far removed from the female atrium. The copulatory bursa appears sac-shaped in sagittal section but extends laterally toward the right posterior intestinal ramus and communicates with it. Bursal canal narrow in its anterior part, widening as it descends behind the male atrium, and equipped with a terminal muscular sphincter. In springs, rivulets, and a cave (J. H. Carpenter, personal communication), Georgia and Alabama. Literature: Darlington (1959).

Phagocata tahoena Kawakatsu, 1968

Synonyms: *Phagocata nivea tahoena* Kawakatsu, 1968; *Fonticola nivea tahoena*: Ball, 1969.

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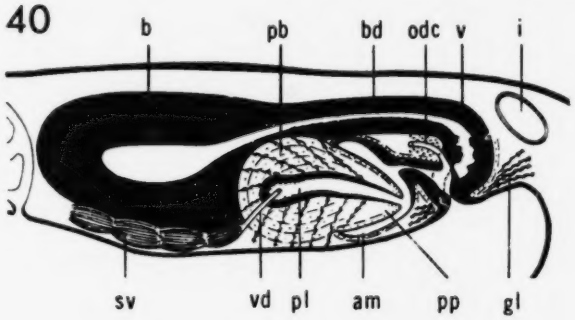

Fig. 40 after Kawakatsu (1968).

A rather plump and thick planarian reaching over 12 mm in length and about 2 mm in width (but may be sexually mature at half that size). Anterior end rounded, frontal margin with a small median projection when the animal is gliding. No neck constriction. Eyes two, at a distance from each other of about 1/3 the width of the head or less. Dorsal side with a brown pigment which fades out toward the lateral margins and leaves a crescent-shaped area along the frontal margin white. Ventral surface unpigmented, white. Testes predominantly ventral, extending from the level of the ovaries to the posterior end. Penis with well-developed bulb and conical or finger-shaped papilla. Penial lumen wide, traversing the penis from the bulb to the tip of the papilla, not clearly differentiated into seminal vesicle and ejaculatory duct. Sperm ducts open separately into the anterior part of the penis lumen. Oviducts uniting above the atrium and opening into its posterior section. Bursa and bursa stalk lined with a very thick epithelium, the stalk running on the left side of the penis and lacking a differentiated vagina. Known only from Lake Tahoe, California and Nevada, at depths of 15 to 1632 feet (4.6 to 500 m). Literature: Kawakatsu (1968), Kenk (1970a).

Phagocata crenophila Carpenter, 1969a

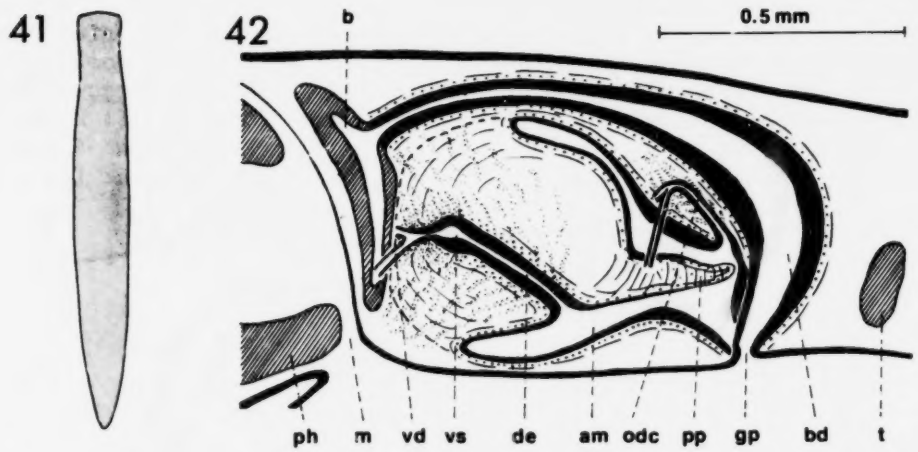

Fig. 42 after Kenk (1970a).

Up to 22 mm long and 2 mm wide. Head truncated, with straight, convex, or slightly wavy frontal margin. Lateral edges rounded, protruding laterally to some extent so that there is a narrowing or neck behind them, rather conspicuous in some populations. Eyes normally two, their distance from each other being about 1/3 the width of the head, the distance of each eye from the lateral margin smaller than from the frontal margin. Dorsal side gray to black, ventral side lighter. Distinguishable from other similar species only by anatomical characters. Testes predominantly ventral, extending posteriorly to almost the tail end of the body. Penis consists of a weakly muscular bulb and a short, rather plump papilla the tip of which is drawn out into a flattened lobe. Sperm ducts enter the bulb anteroventrally and unite within the bulb to a short common vas deferens. This opens into a small cavity, the seminal vesicle, from which a narrow ejaculatory duct proceeds in a posteroventral direction to open on the ventral side of the papilla. The common oviduct opens into the posterodorsal part of the male atrium, the duct of the copulatory bursa ends very close to the gonopore. The most outstanding specific characteristics are the lobular tip of the penis papilla, the configuration of the penial lumen, and the postpharyngeal extension of the testicular zone. In cold mountain springs and streams in the Rocky Mountains and the Sierra Nevada. Literature: Carpenter (1969a), Kenk (1970a).

Phagocata morgani morgani (Stevens & Boring, 1906)

Synonyms: *Planaria truncata* Leidy, 1851; *P. morgani* Stevens & Boring, 1906; *P. albissima*: Kepner & Rich, 1918 (not Vejdovský, 1883); *Dendrocoelum truncatum*: Girard, 1893; *Fonticola truncata*: Hyman, 1931; *F. morgani*: Castle & Hyman, 1934; *F. morgani morgani*: Ball, 1969; *Phagocata morgani*: Hyman, 1937; ?*Dendrocoelum superbum* Girard, 1850; ?*Galeocephala superba*: Stimpson, 1857; ?*Phagocata cavernicola* Hyman, 1954; ?*Fonticola cavernicola*: Ball, 1969.

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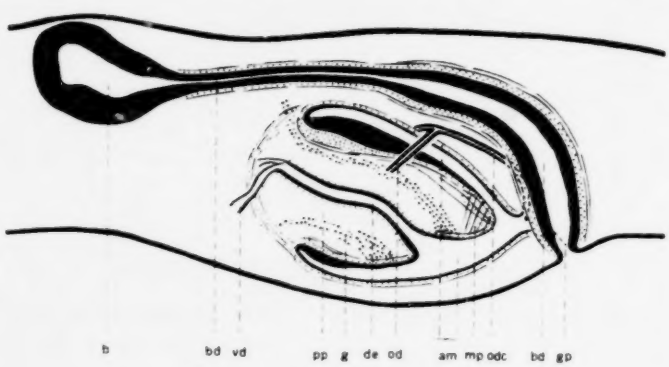

Fig. 44 after Kenk (1935).

Average length of sexually mature specimens 14 mm, width 2 mm. Anterior end truncate, frontal margin straight, convex, or concave when the animal is in motion. No adhesive organ. Lateral edges of head rounded, with a very slight narrowing behind them. Eyes normally two, close together and far removed from the frontal margin. Unpigmented, white. Anterior ramus of intestine ends behind the eye level in adult specimens. Externally similar to *P. nivea* (for differences see that species) and *Planaria occulta* (which has the intestine ending in front of the eyes). Penis with rather small bulb and conical or rounded papilla. Characteristic for the species is a muscular, wart-like structure with thin, flattened epithelium at the tip of the penis papilla. The sperm ducts enter the penial bulb laterally and unite to a generally tubular ejaculatory duct which opens into the atrium on the ventral side of the penis papilla. There is no distinct seminal vesicle developed. Bursa sac-shaped, its duct runs posteriorly, usually to one side (generally left) of the midline, widens gradually without forming a pronounced vagina, and ends close to the gonopore. The common oviduct enters the posterior part of the male atrium near the outlet of the bursal duct. Reproduction sexual and by fission. Cocoon ellipsoidal or spherical, unstalked. Inhabitant of springs and cold creeks of eastern North America from New Brunswick to North Carolina and west to Wisconsin and Kentucky, also found in Taylor Creek, El Dorado County, California (here apparently introduced). Principal literature: Stevens & Boring (1906), Kenk (1935, 1944).

Phagocata morgani polycelis (Kenk, 1935)

Synonym: *Fonticola morgani* var. *polycelis* Kenk, 1935.

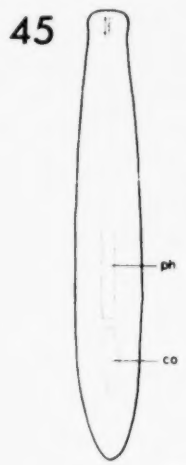

Fig. 45 after Kenk (1935).

Differs from the subspecies *morgani* chiefly in the number and arrangement of the eyes. The eye spots are packed closely together, arranged in a pair of almost parallel longitudinal rows in front of the area covered by the intestine. Their number increases during the growth of the animal from a minimum of 3 on one side in freshly hatched specimens to a maximum of about 40 on the adults. There is no difference between the two subspecies in the anatomy of the reproductive system. Recorded from Virginia and Ontario. Principal literature: Kenk (1935).

Phagocata nivea Kenk, 1953

Synonyms: *Phagocata nivea nivea* Kawakatsu, 1968; *Fonticola nivea nivea:* Ball, 1969.

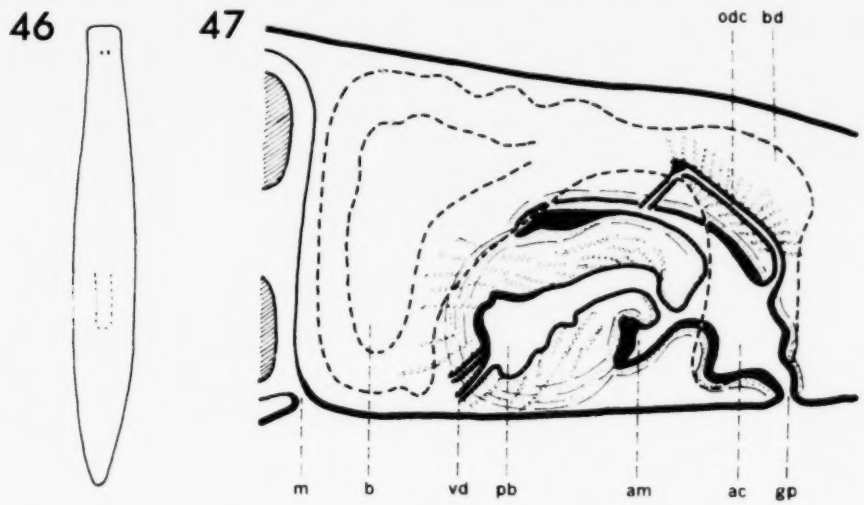

Fig. 47 after Kenk (1953).

Up to 8 mm long and 1.5 mm wide. Head truncated, with slightly bulging frontal margin and rounded lateral corners. No distinct neck. Body unpigmented, white. Eyes normally two, close together, rather far removed from the frontal margin. The species resembles *P. morgani* externally and can be separated from it only by anatomical characters. Testes numerous, predominantly ventral although a few testes may move toward the dorsal side between the branches of the intestine. They are arranged on either side in a zone extending to almost the posterior end (in *P. morgani* this zone ends at the level of the mouth). The penis consists of a spherical bulb and a bluntly conical papilla. The two sperm ducts open separately into the elongated penial cavity which is not clearly divided into a seminal vesicle and an ejaculatory duct, though it gradually narrows posteriorly. It opens into the atrium on the ventral side of the papilla. There is no special muscular differentiation or wart at the tip of the papilla (such as is seen in *P. morgani*). The atrium may appear divided into two chambers, the male and common atria, but this division is not always evident. The two oviducts unite in the space above the male atrium, the common oviduct opening into the atrium posterodorsally. Copulatory bursa large, bursal duct displaced to the left of the midline and surrounded by a coat of intermingled circular and longitudinal muscle fibers (in *P. morgani* it has two separate layers, a circular one adjoining the epithelium and a longitudinal layer). Cold-stenothermic, occurring in mountain streams in Alaska. Literature: Kenk (1953).

Phagocata gracilis (Haldeman, 1840)

Synonyms: *Planaria gracilis* Haldeman, 1840; *Euplanaria gracilis*: Kenk, 1930; *Fonticola gracilis*: Castle & Hyman, 1934; *Phagocata gracilis gracilis* Hyman, 1945; *Fonticola gracilis gracilis*: Ball, 1969; *Phagocata subterranea* Hyman, 1937; *Fonticola subterranea*: Ball, 1969.

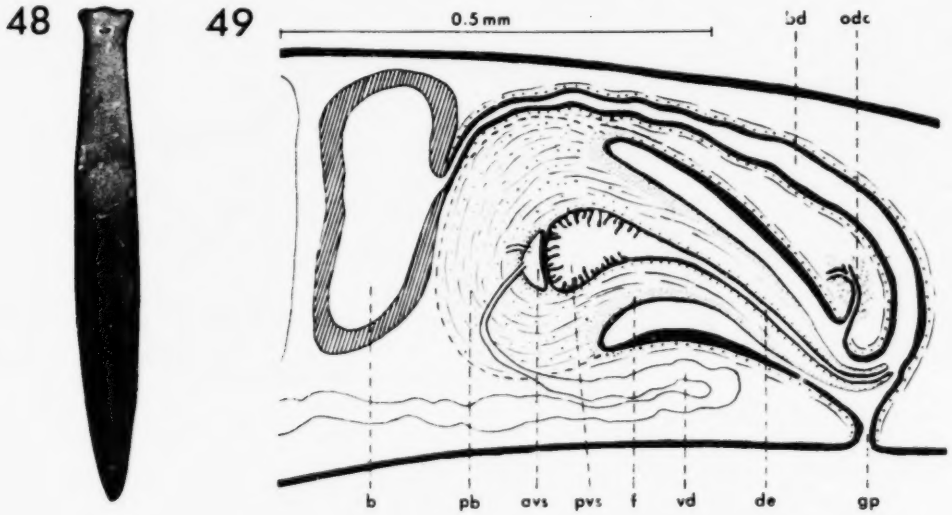

Fig. 49 after Kenk (1970c).

A polytypic species. Mature specimens 8-30 mm long and 1.5-6 mm wide. Head truncated with straight or slightly bulging frontal margin. Generally there is a pair of rounded auricles protruding laterally, but in some populations (in Virginia) these may be subdued. Color generally a shade of gray or brown, darker dorsally than ventrally. In subterranean populations the pigmentation may be almost entirely lacking. Eyes normally two, supernumerary eyes occasionally seen, also eyeless specimens in some subterranean habitats. Pharynges multiple. Testes numerous, predominantly ventral, extending to posterior end. Vasa deferentia with a characteristic backward loop before entering the penis bulb. Penis with highly muscular bulb and elongated pointed papilla. Below the outer epithelium of the papilla is a layer of fine fibers, apparently of an elastic nature, to which longitudinal muscles coming from the bulb attach. Penis lumen divided into two cavities, an anterior nonglandular one and a larger glandular vesicle. The sperm ducts open into the anterior vesicle separately or united. The ejaculatory duct, of variable diameter, proceeds from the posterior vesicle to the tip of the papilla. The muscle coat of the bursal stalk consists of two layers, circular and longitudinal, throughout its length. For differences from *P. woodworthi* see that species. Cocoon spherical or ellipsoidal, unstalked. Reproduction only sexual. Eastern United States south of the Delaware River and west to Missouri. Principal literature: Peaslee (1910), Kenk (1935, 1970c), Hyman (1937a).

Phagocata woodworthi Hyman, 1937a

Synonyms: *Planaria gracilis*: Girard, 1850 (not Haldeman, 1840); *Phagocata gracilis*: Girard, 1850 (and other authors before 1937); *Euplanaria gracilis*: Hyman, 1931 (in part); *Phagocata gracilis woodworthi* Hyman, 1951; *Fonticola gracilis woodworthi*: Ball, 1969.

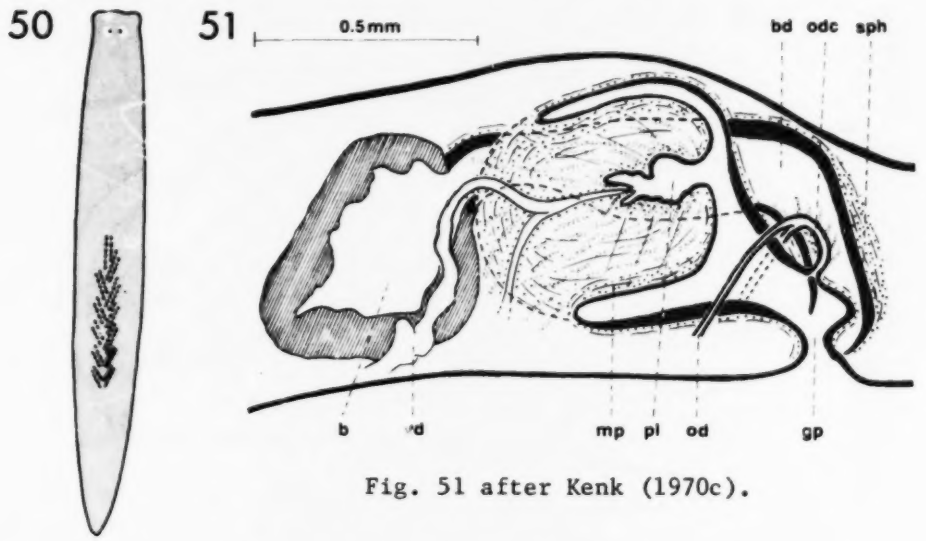

Fig. 51 after Kenk (1970c).

Adult specimens 15-30 mm long and 2-4.5 mm wide. Head truncate, frontal margin assuming a straight, convex, or concave shape during locomotion. Lateral edges of the head rounded, very little protruding laterally. Dorsal side dark gray, brown, or almost black, ventral side lighter. Eyes normally two, situated at a distance of about 1/3 the head width. Pharynges multiple. Cannot be distinguished externally from *P. gracilis*. Testes numerous, mainly ventral (but also dorsal) to the intestine. Vasa deferentia behind the spermiductal vesicles approach the penis bulb directly without forming a backward loop. Penis with feebly muscular bulb and a stout, short, usually truncate papilla. The outer musculature of the papilla consists of a thick layer of intermingled circular and longitudinal fibers very characteristic for the species. Sperm ducts enter bulb anterodorsally or anterolaterally, unite in the bulb and open into the wide penial lumen which is not differentiated into seminal vesicle and ejaculatory duct. The very wide bursal canal is displaced to the right of the midline. It is coated, in the anterior part, by the usual two layers of muscle fibers, circular and longitudinal. As it approaches the atrium near the gonopore, its muscular envelope becomes very thick and consists of intermingled longitudinal and circular fibers. Reproduction probably only sexual. Northeastern parts of the U. S. north of the Delaware River and eastern Canada as far west as Ontario. Principal literature: Woodworth (1891, misidentified as *P. gracilis*), Hyman (1937a), Kenk (1970c).

Sphalloplana percoeca (Packard, 1879)

Synonyms: *Dendrocoelum percoecum* Packard, 1879; *Fonticola percoecum*: Hyman, 1931.

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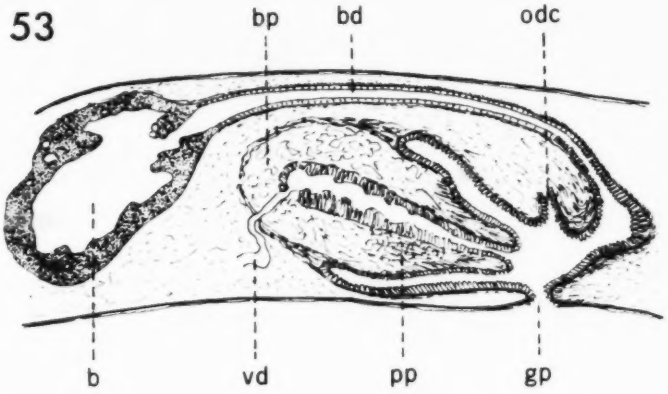

Fig. 52 after Carpenter (1970), modified.
Fig. 53 after Hyman (1937b), modified.

Length up to 16 mm, width about 3 mm. Head truncate, with convex frontal margin and a pair of prominent, rounded auricles projecting anterolaterally. A weak adhesive organ is present in the center of the anterior margin, consisting of a subterminal depression covered with an eosinophilic glandular epithelium to which retractor muscle fibers attach. Eyeless and without pigment, white. Lateral margins of the body with a zone of tall epithelial cells containing long rhabdites. Testes dorsal, prepharyngeal. The penis has a rounded bulb and a conical papilla. The vasa deferentia enter the bulb anterolaterally and open separately into the elongated penial lumen which is not distinctly divided into a seminal vesicle and an ejaculatory duct and opens at the tip of the papilla. The common oviduct enters the genital atrium from the dorsal side at the transition between the male atrium and the small common atrium. The copulatory bursa is sac-shaped, its stalk rather narrow in the anterior portion which passes above the penis and widens only near its opening into the common atrium behind the mouth of the common oviduct. Caves in Kentucky and probably in neighboring states. Principal literature: De Beauchamp (1931), Buchanan (1936), Hyman (1937b).

Sphalloplana alabamensis Hyman, 1945

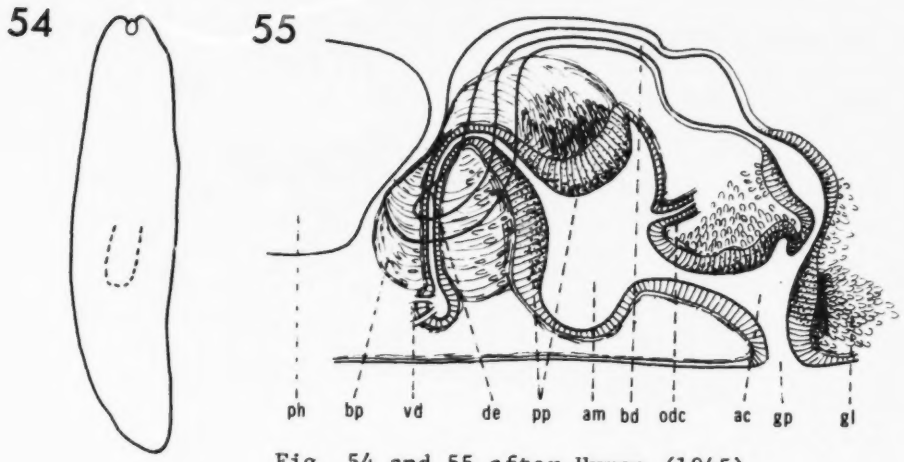

Fig. 54 and 55 after Hyman (1945), modified.

Preserved specimens 5-6 mm long. Anterior end truncate, without auricular extensions. Eyeless, in life presumably white. Body margins with large rhabdites. Adhesive organ at center of frontal margin, consisting of a depression of the epidermis through which eosinophilic glands open, surrounded by an arrangement of mostly radial muscle fibers. Testes rather few, in a pair of longitudinal rows, prepharyngeal. Copulatory complex excessively glandular. Vasa deferentia open into a small chamber (seminal vesicle?) apparently before entering the penis bulb. From this chamber the narrow ejaculatory duct traverses the bulb and the short, rounded penis papilla, widening in the papilla. Epithelium of the papilla tall and glandular. Male atrium separated from the common atrium by a constriction. The common oviduct opens into the posterior part of the male atrium. Copulatory bursa rather small, its duct with irregular enlargements, glandular in its distal portion. Cave in Alabama. Literature: Hyman (1945).

Sphalloplana georgiana Hyman, 1954

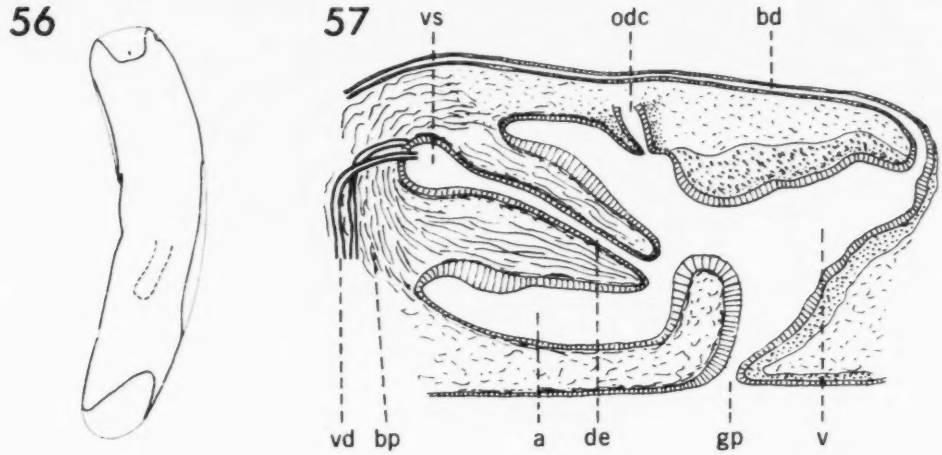

Fig. 56 and 57 after Hyman (1954), modified.

Described from two defective specimens. Preserved animals about 8 mm long. Head truncate, with a central adhesive organ. Blind and unpigmented. Adhesive organ is a subterminal cuplike depression with outlets of eosinophilic glands and longitudinal retractor muscles. Testes small, ventral, forming on either side a band occupying the posterior half of the prepharyngeal region. Penis with muscular bulb and conical papilla. The vasa deferentia enter the bulb ventrolaterally and open separately into a rounded seminal vesicle. This continues posteriorly as a straight ejaculatory duct to the tip of the papilla. The common oviduct opens into the roof of the male atrium. Copulatory bursa not studied. Bursal duct narrow in its anterior portion, proceeding posteriorly beyond the gonopore, then turning abruptly anteroventrally and widening considerably. This widened portion, interpreted best as a vagina, is surrounded by a thick layer of chiefly circular muscle fibers. Known from a cave in Georgia. Literature: Hyman (1954).

Sphalloplana virginiana Hyman, 1945

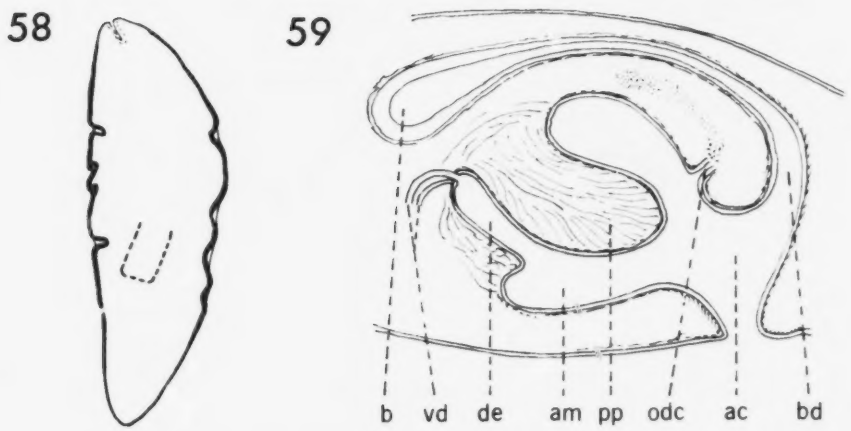

Fig. 58 and 59 after Hyman (1945), modified.

Preserved specimens up to 12 mm long, with bluntly rounded head provided with a central weak adhesive organ. Eyeless and unpigmented. The adhesive organ forms an irregular depression with glandular openings and a band of muscle fibers serving as retractors. Body margins with a rim containing very large rhabdites. Testes ventral and prepharyngeal. Penis with feebly developed bulb and medium-sized, rounded papilla. Vasa deferentia enter separately into the penis lumen which is not subdivided and opens on the ventral side of the papilla. Common ovovitelline duct opens into posterior part of male atrium. Copulatory bursa rather small, bursal duct initially narrow, widening slightly as it approaches the atrium. Known only from a cave in Virginia. Literature: Hyman (1945).

Sphalloplana kansensis Hyman, 1945

60

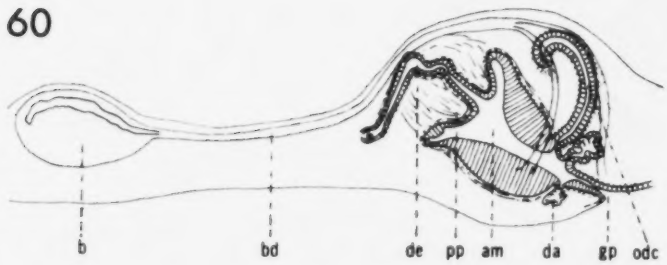

Fig. 60 after Hyman (1945), modified.

Preserved specimens 20 mm long, eyeless, white. Anterior end truncate, with conspicuous adhesive organ. Marginal rhabdites only slightly larger than those of the general epidermis. Adhesive organ consists of a depression with openings of eosinophilic glands and muscular differentiations. Testes dorsal, prepharyngeal. Penis bulb slightly developed, penis papilla rounded, with weak musculature. Sperm ducts unite outside the penis bulb to form a canal, the ejaculatory duct, which after a short sinuous course opens at the center of the penis papilla. Male atrium with very tall epithelium, receiving at its posterior border the long common oviduct. The small common atrium, which connects with the bursal canal, has irregular blind diverticula (important specific characteristic). Bursal canal long, narrow in its anterior section but widening as it approaches the atrium. Known only from a spring in Kansas. Literature: Hyman (1945).

Sphalloplana pricei (Hyman, 1937b)

Synonym: *Speophila pricei* Hyman, 1937.

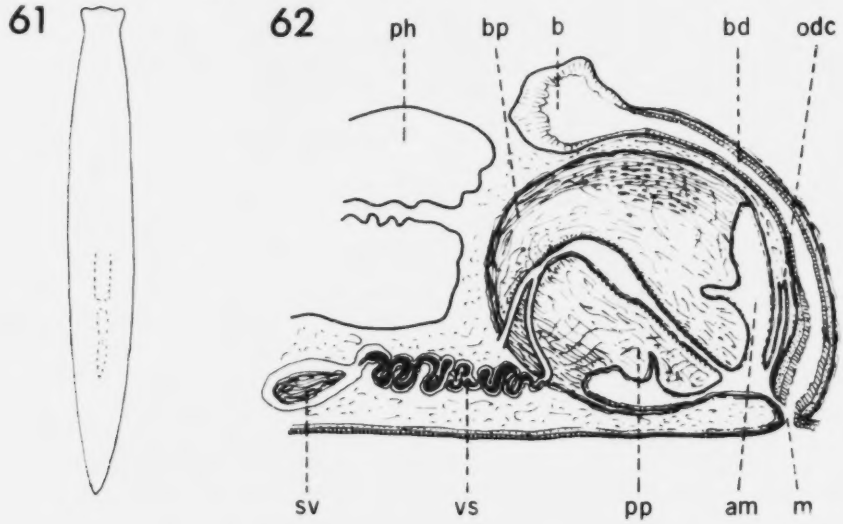

Fig. 62 after Hyman (1937b).

Mature animals up to 28 mm long and 3.5 mm wide. Head truncate, with gently bulging frontal margin and rounded lateral edges (auricles) which in quiet gliding protrude somewhat anteriorly and laterally. Behind the auricles is a constriction or neck. A well-developed adhesive organ forming a deep protrusible invagination with glandular and muscular differentiations is located in the center of the frontal margin. Pigmentless (white) and blind. Lateral margins with a zone of modified epithelium containing very large rhabdites. Testes dorsal, prepharyngeal. Penis with rounded bulb and short, generally conical papilla. Vasa deferentia form spermiductal vesicles at the level of the pharynx, then narrow again as coiled canals and enter the penis bulb separately. In the bulb they unite and soon widen to an elongated seminal vesicle from which an ejaculatory duct proceeds to the tip of the penis papilla. The common oviduct opens into the posterior part of the male atrium. Copulatory bursa of moderate size, bursa duct initially narrow but gradually widens in the posterior portion which opens into the atrium close to the gonopore. Caves in Pennsylvania. Literature: Hyman (1937b).

Sphalloplana buchanani (Hyman, 1937b)

Synonym: *Speophila buchanani* Hyman, 1937.

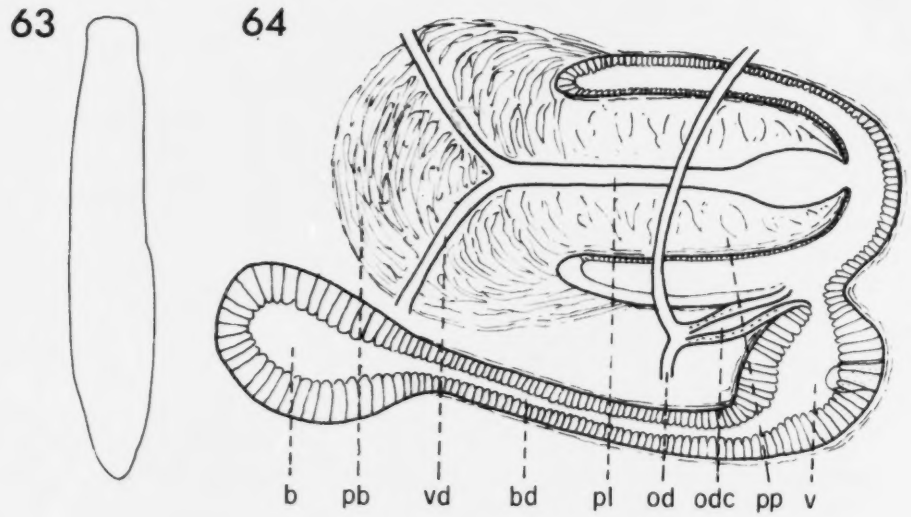

Fig. 63 after Carpenter (1970), modified.
Fig. 64. View from dorsal side (after Hyman, 1937b).

Up to 15 mm long. Anterior end truncate, with a well-developed, protrusible adhesive organ in the middle of the frontal margin, and rounded lateral edges. No distinct narrowing or neck behind the head. Pigmentless and blind. Lateral margins with large rhabdites. Testes dorsal, prepharyngeal. Penis with muscular bulb and well-developed, cylindrical or conical papilla. The sperm ducts enter the bulb and unite to a common canal representing the ejaculatory duct. There is no histologically distinct seminal vesicle, but the duct may show a small widening in its course. Common ovovitelline duct opening into the posterior part of the male atrium. Bursal duct displaced to one side of the midline, seems to be widened in its terminal section. Caves in Kentucky. Principal literature: Hyman (1937b).

Sphalloplana hubrichti (Hyman, 1945)

Synonym: *Speophila hubrichti* Hyman, 1945.

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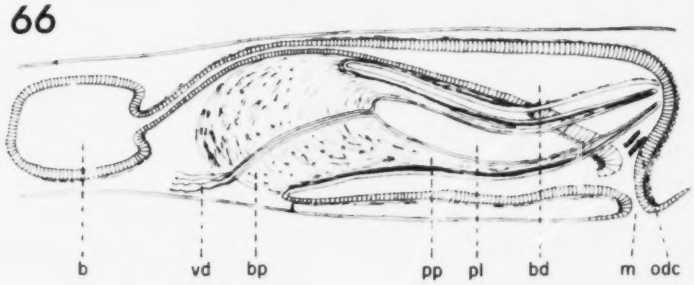
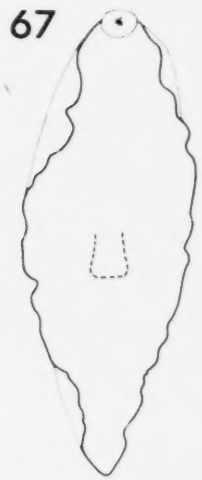


Fig. 65 and 66 after Hyman (1945), modified.

Preserved specimens up to 17 mm long, with broadly rounded anterior end, white, eyeless. Adhesive organ conspicuous, consisting of a deep pit surrounded by many eosinophilic glands and provided with a complex system of muscle fibers. Marginal rhabdites very large. Testes dorsal, prepharyngeal. Penis with muscular bulb and long, finger-shaped papilla. Vasa deferentia unite at the anteroventral border of the penis bulb and traverse the bulb as a narrow canal, the common vas deferens. This opens into a widened, elongated cavity, the penial lumen, which proceeds to the tip of the papilla. Copulatory bursa large. Its outlet runs first above the penis as a narrow canal, then widens considerably while being displaced to the right side of the midline. Caves and springs in Illinois and Missouri. Literature: Hyman (1945).

Sphalloplana hoffmasteri (Hyman, 1954)

Synonym: *Speophila hoffmasteri* Hyman, 1954.



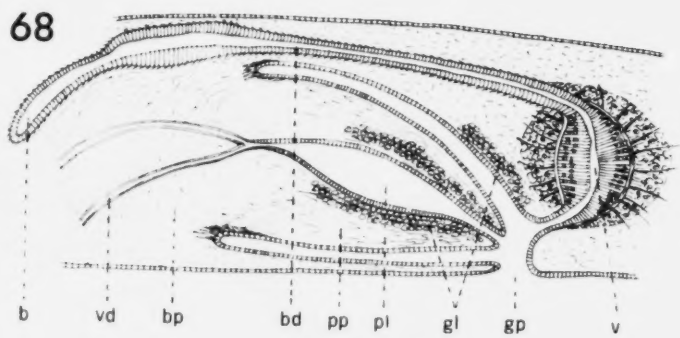


Fig. 67 and 68 after Hyman (1954), modified.

Preserved specimens about 11 mm long, plump. Anterior end rounded, with adhesive organ. Eyeless and white. Lateral margins of the body with a zone of large rhabdites. Adhesive pit is a deep epithelial invagination, with glandular outlets and retractor and protractor muscles. Testes prepharyngeal, rather large, situated on either side of the midline in a band in the middle regions of the sections. Penis with large bulb and elongated, conical papilla. The vasa deferentia enter the bulb and proceed to the base of the papilla where they unite to a short common vas deferens. This empties into the elongated penial lumen which first widens, then narrows again, and opens at the tip of the papilla. The shape of the copulatory bursa is not definitely known. The bursal duct is rather narrow in its anterior course while its distal part, behind the atrium, is differentiated as a vagina with tall epithelial cells and what seem to be muscular structures. Caves in West Virginia. Literature: Hyman (1954).

Sphalloplana weingartneri Kenk, 1970b

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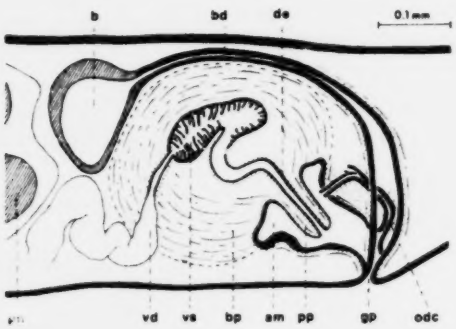

Fig. 70 after Kenk (1970b).

Mature specimens 6-9 mm long and 1.2-1.8 mm wide. Anterior end truncate, with slightly bulging frontal margin and rounded lateral edges, without a neck constriction. Eyeless and unpigmented, white. Body relatively transparent, showing in life the position of the anterior adhesive organ, the pharynx, and in the postpharyngeal part the copulatory complex as a round or elliptical transparent area with an opaque spot in the center. The adhesive organ consists of a deep invagination of the epithelium with irregular outline, which receives the outlets of many eosinophilic glands and to which a system of retractor muscles is attached. Testes numerous, both dorsal and ventral, prepharyngeal. Penis has a large, spherical bulb and a short, finger-shaped papilla. Vasa deferentia enter bulb ventrolaterally and empty separately, but close together, into the elongated, glandular seminal vesicle. From this vesicle a narrower, somewhat curved (contraction?), nonglandular ejaculatory duct proceeds to the tip of the penis papilla. Genital atrium rather small, receiving the common oviduct in its posterior part. Copulatory bursa a rounded sac, bursal duct narrow in its anterior portion, gradually widening as it curves down toward the gonopore but showing no histologically distinct vagina nor a terminal sphincter. Found in a cave in Indiana. Literature: Kenk (1970b).

Sphalloplana mohri Hyman, 1939c

Synonyms: *Sphalloplana kutscheri* Mitchell, 1968; *S. sloani* Mitchell, 1968; *S. zeschi* Mitchell, 1968; *S. reddelli* Mitchell, 1968.

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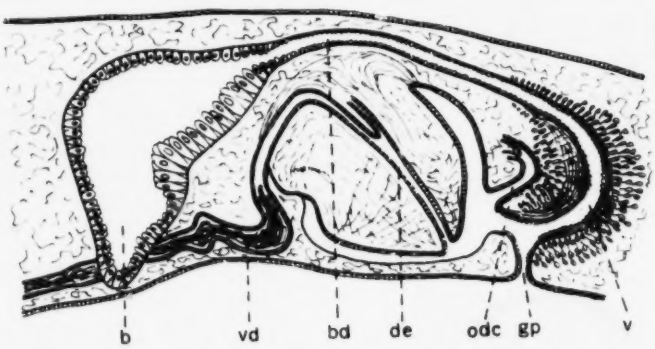


Fig. 71 after Carpenter (1970), modified.
Fig. 72 after Mitchell (1968), modified.

Mature animals 20-35 mm long and 3-5 mm wide. Anterior end truncate, with laterally protruding auricles. The glandular and muscular adhesive organ, deeply invaginated when at rest, may be extended as a conical projection through its opening at the center of the frontal margin. Behind the auricles the head narrows to a neck, then the body widens again. Eyeless and without pigment, white. Polypharyngeal, with up to about 50 pharynges. Testes relatively few, situated between the intestinal branches, extending back to the level of the anterior pharynges. Penis consists of a bulb of moderate size and a larger cylindrical or conical papilla, both with feeble musculature and easily distorted in preservation. The vasa deferentia enter the bulb anterolaterally and unite in the penis papilla. The common vas deferens may show a widened section, the equivalent of a seminal vesicle, and continue as ejaculatory duct to the tip of the papilla. The common ovovitelline ducts open into the posterior part of the male atrium (there is hardly any common atrial cavity developed). Bursal duct with a narrower anterior section and a wider, thick-walled, glandular and muscular terminal portion (vagina). Caves in Texas. Principal literature: Hyman (1939c), Mitchell (1968).

Kenkia rhynchida Hyman, 1937b

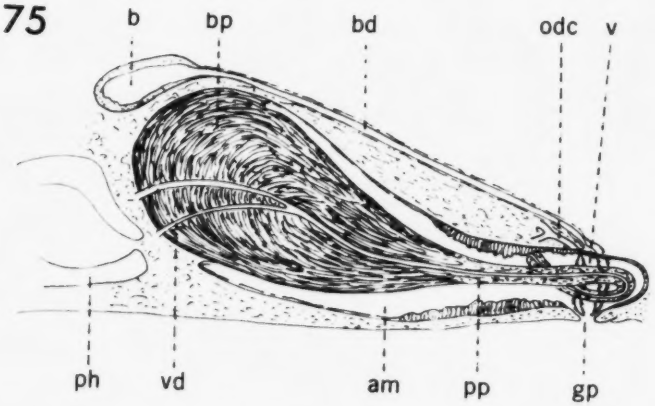
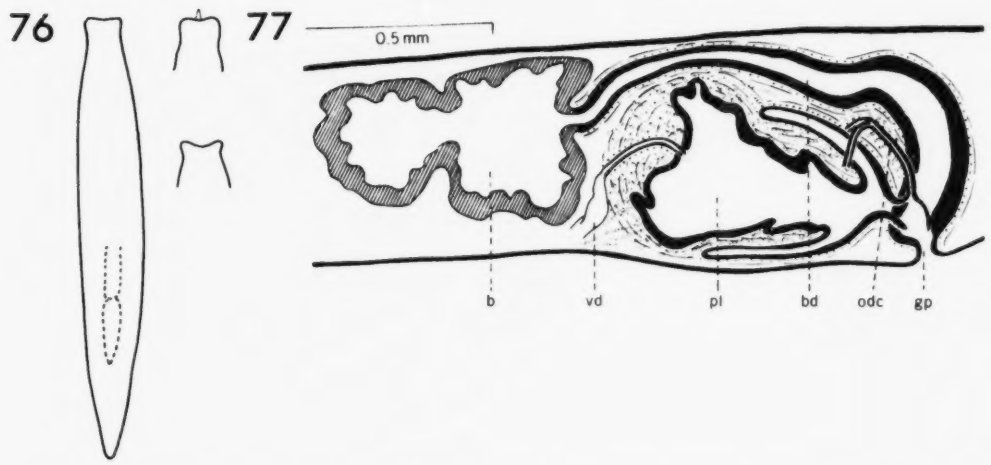


Fig. 73 and 74. Ventral and lateral views of preserved specimen (after Hyman, 1937b). Fig. 75 after Hyman (1937b).

Has not been studied in detail in life. Living specimens about 1/4 inch (6 mm) long, of oval-domed shaped, white, with a creamy center. Preserved animals 2-4 mm long, of oval outline, with a convex dorsal and a concave ventral surface, described as being of the shape of a miniature turtle. At the anterior end is a snout-like projection, cylindrical in cross section, containing a deep epithelial invagination with glandular and muscular differentiations, apparently serving as an adhesive organ. The postpharyngeal region is much reduced in size. Eyes are absent. The lateral margins of the body have a thick band of very large rhabdites. Testes few, large, forming on either side a group located dorsolaterally in the middle of the prepharyngeal region. Copulatory apparatus close to posterior end. Penis with spherical bulb and elongated papilla which is conical at its base and cylindrical in the distal part. The vasa deferentia enter the penis bulb, unite, and continue as a narrow canal, the ejaculatory duct, to the tip of the penis papilla without forming an enlargement or seminal vesicle. Copulatory bursa small, with narrow stalk enlarged only in the distal portion close to the gonopore. Common oviduct opens into posterior part of male atrium. Known only from Malheur Cave, Harney County, Oregon. Literature: Hyman (1937b).

Macrocotyla glandulosa Hyman, 1956



(Hyman's description emended by study of additional material). A large species, up to 30 mm long and 6 mm wide. Anterior end truncate, with straight or slightly waved frontal margin and rounded lateral edges which protrude only little to the sides, causing a faint incurving to appear behind them. A protrusible adhesive organ may be projected from the center of the frontal margin during searching movements or upon stimulation. Eyes lacking. Color in life a very light reddish-brown or orange. The pigment is not granular but is diffused in the subepidermal tissues, including the head and the body margins, absent only in the pharynx, the copulatory complex, and the denser parts of the adhesive organ. Lateral margins with large rhabdites. Testes ventral, prepharyngeal. Penis with large bulb and conical papilla, flanked by voluminous masses of eosinophilic glandular tissue which empty their secretions into the penis lumen. The penis bulb contains a large cavity with irregular folded outline, the seminal vesicle. From this cavity a rather wide canal, the ejaculatory duct, proceeds to the tip of the papilla. The sperm ducts open into the seminal vesicle independently, without uniting. Common oviduct connects to the posterior part of the male atrium. Copulatory bursa relatively large, with wide outlet opening near the gonopore. Reproduction sexual, with spherical egg capsules of over 3 mm diameter, unstalked. The species resembles a *Sphalloplana* in all essential characteristics except the arrangement of the pharyngeal muscle fibers, which is of the dendrocoelid type (see p. 13). Caves (J. H. Carpenter, personal communication) and spring in Missouri and Iowa. Literature: Hyman (1956).

Dendrocoelopsis vaginata Hyman, 1935

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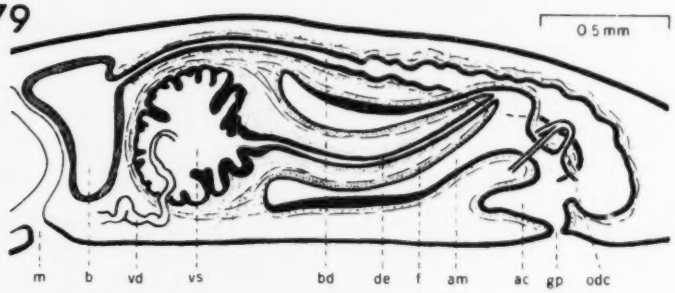
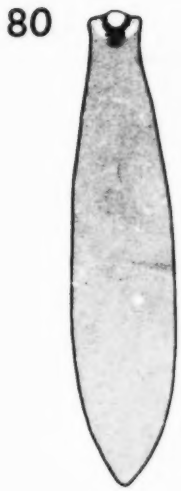


Mature specimens 14-22 mm long and about 3 mm wide. Head truncate, with gently bulging frontal margin, a weak subterminal adhesive organ, rounded corners, and a slight narrowing (neck) behind them. Eyes usually two, their distance from each other about 1/3 the width of the neck, the distance of each from the frontal margin a little larger than from the lateral margin. Dorsal side gray or brown, ventral surface somewhat lighter (the pigment bleaches easily after preservation). Pigment absent from the two eye fields, a point near the mouth, and a circular area around the gonopore. A pair of somewhat lighter oblique streaks on the head laterally to the eyes. Similar to *D. piriformis* but with different body outline (largest width is reached in the prepharyngeal region). Testes numerous, ventral, reaching to level of gonopore (in *D. piriformis* dorsal, to posterior end). Penis with large spherical bulb and finger-shaped papilla. The bulb contains a large, round, highly glandular seminal vesicle and receives the two sperm ducts ventrolaterally. From the vesicle a narrower ejaculatory duct proceeds to the tip of the papilla. Below the flattened outer epithelium of the penis papilla is a dense fibrous layer followed by a layer of longitudinal muscles. The outlet of the copulatory bursa widens as it proceeds posteriorly and gradually acquires a folded outline. It opens into the atrium close to the gonopore. Egg capsule spherical, about 1.6 mm in diameter. Springs, streams, and lakes in Montana, Oregon, and Washington. Literature: Hyman (1935).

Dendrocoelopsis piriformis Kenk, 1953



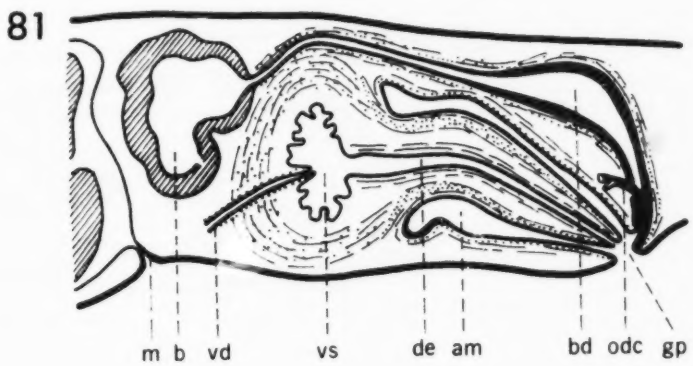


Fig. 81 after Kenk (1953).

A rather broad and plump species, up to 15 mm long and 3 mm wide. Head truncated, with a bulging central portion of the frontal margin indicating the site of the adhesive organ. In quiet gliding the greatest width of the body is reached at the beginning of the last third. A pair of rounded auricles protrude only little laterally, with a shallow constriction behind them. When resting, the body appears pear-shaped, the lateral margins often showing a ruffled outline. Eyes usually two, situated at a distance of about 1/3 the width of the head. Pigmentation dorsally brown or gray, with a dark field between the eyes and extending to the frontal margin on both sides of the adhesive organ which itself is unpigmented. There may be one median and often a pair of additional lateral longitudinal dark stripes along the body. Ventral side lighter gray. Pharynx short, of the dendrocoelid type. Testes numerous, dorsal, arranged in a pair of wide bands reaching close to the posterior end (in the similar *D. vaginata* the testes are ventral). Penis with large, spherical bulb and long, finger-shaped, pointed papilla. Sperm ducts enter the bulb anterolaterally and open into the seminal vesicle independently, each on a conical projection. Seminal vesicle large, with glandular wall of irregularly lobed outline. Ejaculatory duct narrow and long, opening at tip of penis papilla. Common oviduct opens into atrium close to gonopore. Bursa and bursal canal without peculiarities. Inhabitant of lakes and streams in Alaska and northwestern Canada. Principal literature: Kenk (1953), Holmquist (1967).

Dendrocoelopsis alaskensis Kenk, 1953

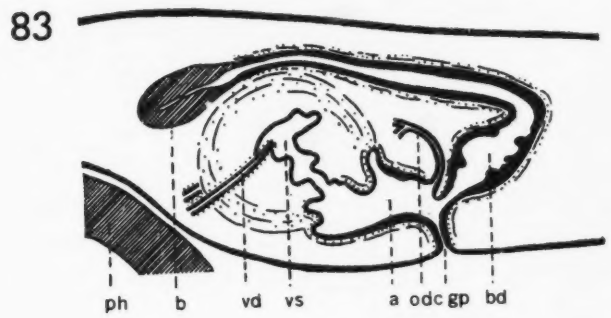


Fig. 83 after Kenk (1953).

A large, white species, not yet studied at full maturity. Largest specimen examined 20 mm long and 4 mm wide. Anterior end truncated, with slightly convex central part of the frontal margin flanked by rounded auricles protruding anteriorly and laterally. No distinct adhesive organ. Eyes normally two, separated by about 1/3 the width of the head and nearly equidistant from the frontal and lateral margins. There sometimes are smaller accessory eyes developed in front of or behind the principal eyes. The description of the reproductive system is based on the examination of one specimen which was not fully mature. Primordia of the testes predominantly ventral, traceable posteriorly to the level of the mouth (they possibly may extend farther back in fully mature animals). Penis with spherical bulb and short papilla. Vasa deferentia open separately into the penial lumen. Penis cavity in wide communication with the undivided genital atrium. Common oviduct opens into atrium anterior to the opening of the bursal duct. In springs and cold creeks in Alaska. Literature: Kenk (1953).

Dendrocoelopsis hymanae Kawakatsu, 1968

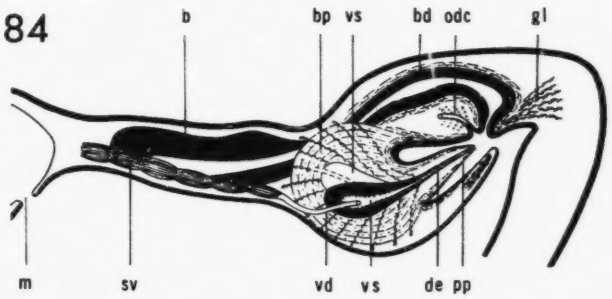


Fig. 84 after Kawakatsu (1968).

Has not been studied in life. Description was prepared from one mature and one immature specimen in defective condition. Unpigmented (in life "translucent pink"), eyeless, up to 14 mm long and 2 mm wide. Anterior end with subterminal adhesive organ forming a depression with glandular and muscular differentiations. Testes numerous, of moderate size, ventral, extending posteriorly to the base of the pharynx. Penis with highly muscular spherical bulb and conical pointed papilla. Seminal vesicle divided into a pair of elongated cavities, each receiving one of the sperm ducts anterolaterally. The two cavities unite at the base of the papilla from where a rather narrow ejaculatory duct proceeds to the tip of the papilla. The common oviduct opens into the posterior part of the male atrium from the dorsal side. There is no common atrium developed. The outstanding specific characteristics are the lack of eyes and the division of the seminal vesicle. Known only from Lake Tahoe, California and Nevada, from a depth of about 1600 feet. Literature: Kawakatsu (1968).

Dendrocoelopsis americana (Hyman, 1939a)

Synonym: *Sorocelis americana* Hyman, 1939.

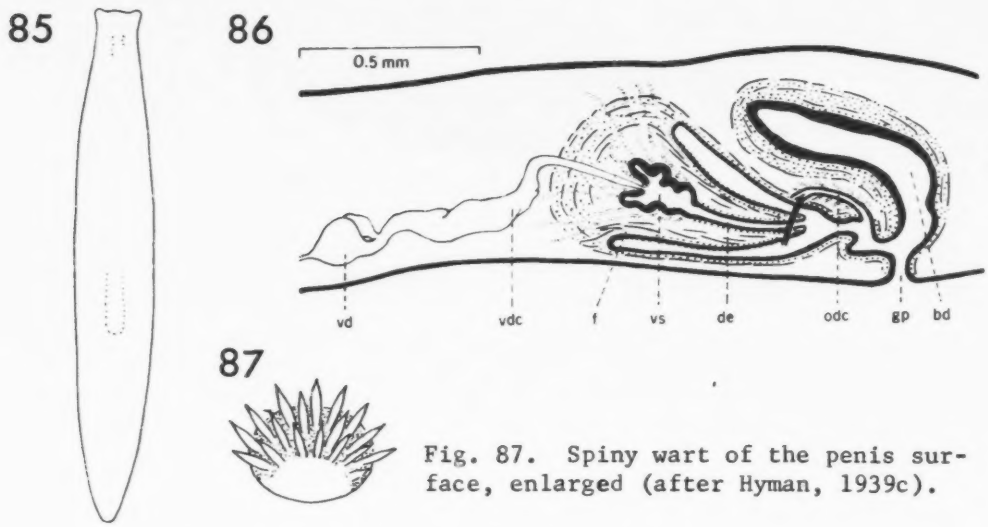


Fig. 87. Spiny wart of the penis surface, enlarged (after Hyman, 1939c).

Up to 18 mm long and 2 mm wide. Anterior end of quietly gliding animal truncate, with convex frontal margin, laterally and anteriorly protruding auricular appendages, and a distinct narrowing or neck behind the auricles. Adhesive organ subterminal, weakly developed. Eyes numerous, arranged in two almost parallel longitudinal rows placed at a distance from each other of about 1/3 the width of the neck region. Number of eyes increases during growth. Body unpigmented, white. Testes not numerous, predominantly dorsal, extending posteriorly to behind the copulatory complex. Sperm ducts unite at a variable distance anterior to penis. Penis with muscular rounded bulb and conical papilla. The common vas deferens enters the bulb anteriorly, traverses the bulb as a straight narrow canal and opens into a highly glandular cavity with irregular outline, the seminal vesicle. From there the narrow ejaculatory duct runs to the tip of the penis papilla. Cells of the outer epithelium of the papilla appear as wartlike eminences, each studded with colorless, pointed spines (this can be seen on the freshly extirpated penis). Common oviduct opens into the posterior end of the male atrium. Copulatory bursa absent, bursal canal blindly closed and covered by a thick layer of muscles. Cocoon almost spherical, unstalked. Inhabits caves and springs in Oklahoma and Arkansas. Literature: Hyman (1939a, 1939c).

Procotyla fluviatilis Leidy, 1857

Synonyms: *Dendrocoelum superbum*: Leidy, 1851 (not Girard, 1850); *D. lacteum*: Woodworth, 1896 (not O. F. Müller, 1774); *D. graffi* Wilhelmi, 1909; ?*D. pulcherrimum* Girard, 1850; ?*Oligocelis pulcherrima*: Stimpson, 1857.

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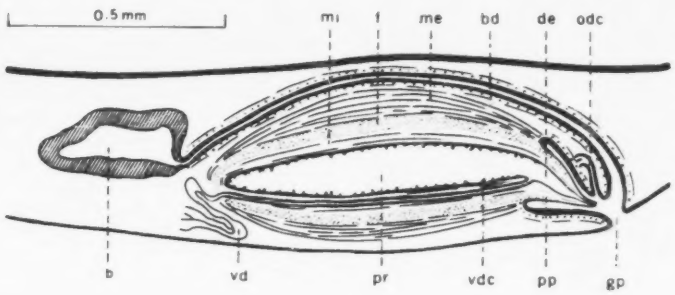

Mature animals 12-20 mm long and 2-5 mm wide. Head truncated, rather variable in shape during locomotion. Subterminal adhesive organ clearly visible in living animal, bulging out slightly during gliding, flanked by two rounded auricular projections with a constriction or neck behind them. Eyes of variable number, in the northern distributional area 1-8 on either side, in the sourthern states usually only 1. The groups of eyes are rather far removed from each other, by about 1/2 the width of the head. Testes numerous, dorsal, extending posteriorly to level of copulatory complex. Vasa deferentia unite at the level of the penis and enter the penis bulb anteroventrally as common vas deferens. The penis consists of an elongated muscular bulb with a large cavity and a short conical papilla. The bulb is composed of several layers surrounding the cavity: an outer, very thick layer of longitudinal muscles, a fibrous layer, an inner layer of chiefly longitidinal muscle fibers (in *P. typhlops* these are circular), and the glandular epithelial lining of the cavity or prostate. The common vas deferens runs along the ventral wall of the penial cavity and connects with it at the base of the penis papilla. Beyond this junction the lumen continues into the penis papilla as ejaculatory duct and opens at its tip. The common oviduct and the outlet of the sac-shaped copulatory bursa open close to the gonopore. Cocoon ellipsoidal, unstalked. The species refuses liver or *Tubifex* as food but takes living amphipods, isopods, and aquatic insect larvae. Inhabits ponds, lakes, streams and springs in the eastern part of North America, from Maine to Louisiana and west to Ontario, Wisconsin, and Illinois. Principal literature: Woodworth (1897), Hyman (1928), Kenk (1944).

Procotyla typhlops Kenk, 1935

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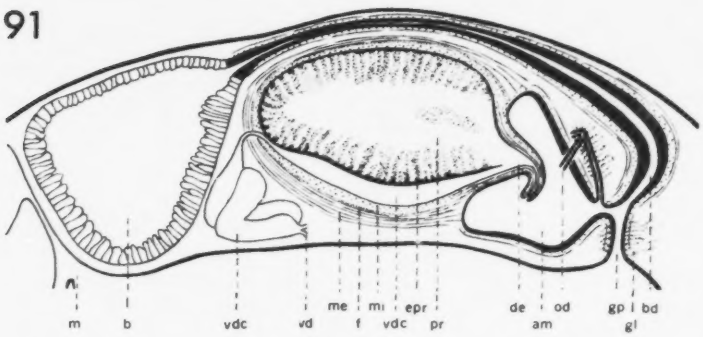

Fig. 91 after Kenk (1935).

A small, slender species, up to 12 mm long and 1.3 mm wide. Head truncate, with straight or slightly convex frontal margin, rounded lateral edges, and an insignificant narrowing behind them. No distinct adhesive organ. Eyeless and white. Testes numerous, predominantly dorsal, extending posteriorly to the region of the pharynx. Vasa deferentia, after passing through the spermiductal vesicles, unite outside the penis bulb to a common sperm duct which is also sinuous and expanded. The penis consists of a large, elongated, muscular bulb and a short, conical papilla. The common vas deferens enters the anterior part of the bulb and continues the entire length of the bulb ventrally to a large, glandular cavity with which it communicates at the base of the papilla. The role of this cavity is probably that of a prostatic gland adding its secretions to the sperm passing through the sperm duct. The wall of the penis bulb has three layers: an outer, thick layer of approximately longitudinal muscle fibers, a thin fibrous layer, and an inner layer of circular muscles. The lumen of the penis papilla, representing the ejaculatory duct, tapers toward the tip of the papilla where it opens into the atrium. The copulatory bursa is typical, sac-shaped, its duct at first rather narrow but gradually widening posteriorly without a histologically differentiated vagina. Apparently a subterranean species found in springs and groundwater pools in Virginia (a two-eyed form alleged to be this species has been reported from Florida, but this record needs confirmation). In the laboratory the species accepts liver and *Tubifex* as food. Literature: Kenk (1935).

Rectocephala exotica Hyman, 1953b

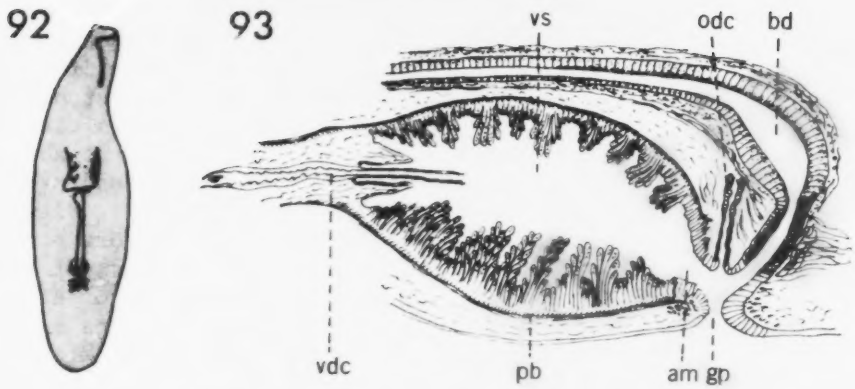

Fig. 92 and 93 after Hyman (1953b).

Preserved specimen 14 mm long. Anterior end appears to be truncate, with a central adhesive organ. Eyes two. Pigmentation uniformly black. Adhesive organ forms an irregular invagination of glandular epithelium, equipped with a complex system of muscle fibers. Ovaries rather far back from the head, testes not seen. Copulatory complex consists chiefly of a large cavity lined with a tall glandular epithelium which forms villus-like projections. This cavity is interpreted by Hyman as an enlarged bulbar lumen. The sperm duct (called ejaculatory duct by Hyman), apparently originating from the union of the paired ducts, enters the anterior wall of the cavity and projects into its lumen. The common oviduct opens into the posterior sector of the male cavity which is lined by a normal, nonglandular epithelium (interpreted as the remnant of a male atrium). The copulatory bursa, situated behind the pharyngeal pouch, has an exceedingly long, narrow canal running backward in the dorsal midline, widening only in its posterior portion, then narrowing again and opening into the atrium near the gonopore. Only one specimen has been studied, collected in the Shaw Lily Ponds (now Kenilworth Aquatic Gardens), Washington, District of Columbia, apparently introduced with exotic water plants. Literature: Hyman (1953b).

Planaria simplex Woodworth, 1896a . Described from one immature specimen of 4 mm length and 1.8 mm width, of ovate shape. "Anterior end rounded, set off from the rest of the body by slight lateral indentations at the level of the eyes, i. e. at about 1/10 total length from the anterior end. No evidence of cephalic appendages. ... Pigment located in spots of nearly uniform size, distributed uniformly over all parts of the body; no clear areas surrounding eyes or at sides of head. Color of alcoholic specimen ochre-yellow." Dredged off New York Point, Lake Michigan (on Grand Traverse Bay, Michigan). Literature: Woodworth (1896a, 1896b).

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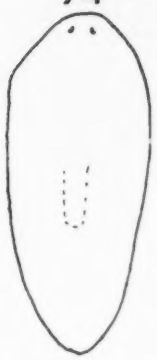

After Woodworth (1896b).

Planaria fuliginosa Leidy, 1851 . Synonyms: *Planaria (Typhlolepta?) fuliginosus* Leidy, 1851; *Anocelis fuliginosa*: Stimpson, 1857. "Body oval, dilated; inferiorly flat; superiorly moderately convex, fuliginous. Eyes none: in their ordinary position a slightly greater accumulation of black pigment upon the upper surface. Mouth inferior, a little posterior to the centre; oesophagus simple, cylindrical, white, 1 line long by 1/2 line broad." Length 8 mm, breadth 6 mm (extended?). Rancocas Creek near Pemberton, Burlington County, New Jersey. Literature: Leidy (1851), Girard (1893).

Planaria unionicola Woodworth, 1897 . Described from one specimen which apparently had been sketched in life by the collector and had been brownish red, mottled with purplish dots (color of intestinal contents?). According to the sketch the head is truncate, with a sinuous frontal margin. The two eyes show large circular periocular fields. The posterior end is blunt, suggesting either an injury or recent fission. After preservation the specimen was much contracted and shriveled, 2.8 mm long and 1.8 mm broad. Collected on the mantle of *Unio* in the Illinois River near Havana, Illinois. Literature: Woodworth (1897).

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After Woodworth (1897).

Hydrolimax bruneus Girard, 1891 . Length 19 mm, width 3 mm. Head obtusely truncate, with a neck constriction behind it. Eyes two, Body dark brown, head somewhat lighter. Intestinal coecum reaches anteriorly between the eyes. Genital opening anterior to the middle of the body, with a thickening at its level caused by the presence of eggs or cocoons. Found in a small stream in Fairmount Park, Philadelphia, Pennsylvania. This may be one of the brown species of *Phagocata*, or *Hymanella*, or may not be a triclad. Literature: Girard (1891, 1893).

After Girard (1893).

SECTION V

ABBREVIATIONS USED ON FIGURES

The figures of the copulatory apparatus are diagrams reconstructed from adjoining sagittal sections. Their orientation is with the anterior parts to the left. In the outline drawings, pigmented species are indicated by shading, unpigmented species are white.

Abbreviations used are as follows:

a	genital atrium or antrum
aa	atrium of adenodactyl
ac	common atrium or antrum
ad	adenodactyl
af	female atrium or antrum
ai	anterior intestinal ramus
am	male atrium or antrum
ao	adhesive organ
au	auricle
avs	anterior seminal vesicle
b	copulatory bursa or bursa copulatrix
bd	bursal duct, canal, or stalk
bg	glandular portion of bursal canal
bp	penial bulb
br	brain or cerebral ganglion
cg	cyanophilic glands
co	copulatory apparatus or complex
de	ejaculatory duct
dp	diverticulum of penial lumen
eg	eosinophilic glands
epe	external epithelium
epi	internal epithelium
epr	epithelium of prostate
f	fibrous layer
gl	glands
gp	gonopore or genital aperture
i	intestine or gut
m	mouth or oral aperture
me	external muscle layer
mi	internal muscle layer
mp	muscles of penis papilla
n	ventral nerve cord
od	oviduct or ovovitelline duct
odc	common oviduct or common ovovitelline duct
ov	ovary
pa	parenchyma
pb	penis bulb
ph	pharynx
pi	posterior intestinal ramus
pl	penial lumen
pp	penis papilla
pr	prostate
pvs	posterior seminal vesicle
r	margin with large rhabdites
sg	shell glands
sn	snout
sph	sphincter
sv	spermiductal vesicle or false seminal vesicle
t	testis
v	vagina
vd	vas deferens or sperm duct
vdc	common vas deferens
vi	vitellaria or yolk glands
vs	seminal vesocle

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SECTION VI

ACKNOWLEDGMENTS

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